

4898

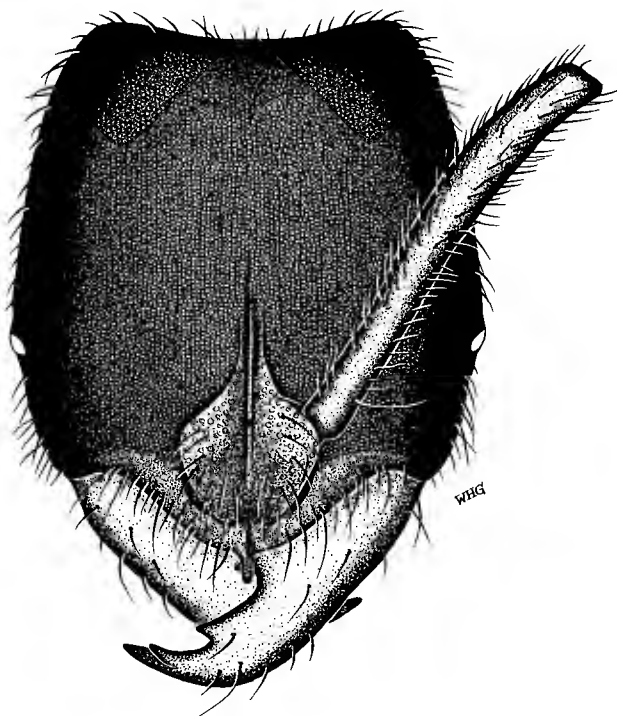
WILLIAM L. DROWN

MEMOIR 408**

July 1969

Comparative Morphological Studies of the Ants, with Particular Reference to the Mouthparts (Hymenoptera: Formicidae)

William H. Gotwald, Jr.



Cornell University

AGRICULTURAL EXPERIMENT STATION

New York State College of Agriculture, Ithaca, N.Y.

Contents

Methods	4
Mouthpart preparations	4
Gaster preparations	5
Method of illustration	5
Results of investigation	5
General features of ant mouthparts	5
Labrum	6
Mandibles	7
Maxillae	8
Labium, hypopharynx, epipharynx, and infrabuccal pocket	9
Comparative survey of mouthparts of representative species	20
Family Tiphidae	20
Subfamily Methochinae	20
Subfamily Thynninae	21
Family Formicidae	25
Subfamily Ponerinae	25
Subfamily Cerapachyinae	43
Subfamily Dorylinae	49
Tribe Aenictini	49
Tribe Dorylini	55
Tribe Cheliomyrmecini	68
Tribe Ecitonini	73
Subfamily Leptanillinae	97
Subfamily Myrmicinae	99
Subfamily Myrmeciinae	113
Subfamily Pseudomyrmecinae	116
Subfamily Dolichoderinae	118
Subfamily Formicinae	120
Condition of gastral sclerites in representative species	126
Subfamily Ponerinae	126
Subfamily Cerapachyinae	126
Subfamily Dorylinae	127
Subfamily Myrmicinae	127
Subfamily Myrmeciinae	128
Subfamily Pseudomyrmecinae	128
Subfamily Dolichoderinae	128
Subfamily Formicinae	128
Discussion	129
Mouthpart morphology and function	129
Fusion of gastral sclerites	134
Phylogenetic considerations	134
Conclusions	142
Literature cited	144
Acknowledgments	150

Received for publication August 27, 1968

Comparative Morphological Studies of the Ants, with Particular Reference to the Mouthparts (Hymenoptera: Formicidae)¹

William H. Gotwald, Jr.*

The ants are social insects that occupy a diverse range of habitats and yet maintain a relatively uniform habitus. Taxonomists generally consider them as a single family, Formicidae, in the unifamilial aculeate hymenopteran superfamily Formicoidea. Wheeler recognized 7 formicid subfamilies and later suggested an eighth, the Leptanillinae (1923), but as many as 15 have been proposed by Clark (1951). Brown (1954) reviewed the phylogeny of the ants and recognized 9 subfamilies. However, the phylogeny and subfamilial classification of the ants are, in the opinion of myrmecologists, highly speculative, and require the study of many neglected lines of evidence. The present investigation attempts to add significantly to 2 of these lines, and to apply the new facts to the theory of formicid phylogeny.

The mouthparts and the sclerites of gastral segments 1 and 2 are here analyzed morphologically in representatives of major ant groups with the purpose of determining how the nature of these structures reflects on past and recent interpretations of ant phylogeny and classification. Particular emphasis has been placed on the subfamily Dorylinae, because its own phylogeny presents many intriguing questions regarding the possible role of convergence, particularly in foraging behavior, in ant evolution.

In the study of the mouthparts, 104 species of ants were examined, and in the study of the gaster, 80 species were examined. For several species of the subfamily Dorylinae, the mouthparts of workers, both soldiers and medias, and of males and queens were studied. The mouthparts of females of 3 species of Tiphidae were also examined. A tiphoid ancestor has consistently

¹Adapted from a thesis submitted to the Faculty of the Graduate School of Cornell University, August 1968, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

* Former graduate research assistant, Department of Entomology and Limnology, Cornell University, Ithaca, New York. Presently assistant professor, Department of Biology, Utica College of Syracuse University, Utica, New York 13502.

been hypothesized for the ants (e.g., Brown, 1954; Wilson, Carpenter, and Brown, 1967), so comparison of tiphid and formicid mouthparts was considered relevant to this investigation.

Methods

Mouthpart Preparations

Although fresh specimens or specimens preserved in alcohol were preferred for the examination of the mouthparts, dried specimens were used where necessary, and were relaxed by immersing them in a solution of distilled water, 95 percent ethyl alcohol and trisodium phosphate, for 24 hours or longer. After relaxation the specimens were transferred to 70 percent ethanol. The mouthparts of specimens relaxed in this way suffered little distortion or damage to any of the structures studied, except the glossa. This primarily membranous structure was usually deformed even in materials preserved in alcohol. In preparation for study, the mouthparts were first entirely removed from the head capsule of the specimen and were separated into individual components or combinations of components. These were usually as follows: the labium; 1 labial palp; the galea and lacinia; the stipes, cardo, and maxillary palp; the labrum; and each of the mandibles. In smaller specimens the maxillae were left intact, and the palpi were left attached to the labium.

After dissection, the mouthparts were dehydrated and stained with a 0.5 percent solution of eosin Y in 95 percent ethanol. The labrum and mandibles were dehydrated without staining. After 10 minutes of dehydration and staining, the mouthparts were placed in clove oil for a minimum period of 20 minutes. Each component or group of components was then mounted on a microscope slide in Canada balsam. A degree of structural distortion was produced in some of the mouthpart components by the pressure applied to the cover glass, because structures had necessarily to be positioned and partially flattened for thorough observation. This was particularly true for the galea, which had to be flattened from its curved spatulate form. The labium was also subject to distortion in balsam mounts, and it was necessary to preserve some of the largest labia in small vials of glycerin. But in all instances distortion was kept at a minimum, and its effects were taken into account in the subsequent morphological observations.

Voucher specimens (either the specimens dissected, specimens from the same nest series as those dissected, or specimens compared with those dissected) have been deposited in the Museum of Comparative Zoology, Harvard University. Each pin of voucher specimens is indicated as such by a green label that reads: *Voucher specimen, Gotwald study, 1968.*

Gaster Preparations

The gasters of most species whose mouthparts were examined were dissected to determine the degree of fusion of sternite to tergite in both the first and second gastral segments. These dissections can be performed easily, and in many species; e.g. the dolichoderines and formicines, the degree of fusion or nonfusion can be determined without dissection. The dissection itself consists merely of pulling the tergites and sternites apart to ascertain whether they are securely fused or are connected only by membrane. Generally the relationship of these sclerites to one another is obvious; but in some species the tergites and sternites are tightly joined in such a way as to be intermediate between fusion and nonfusion.

Method of Illustration

All drawings were done by the author, and most were made with the use of a Bausch and Lomb VH type micro-projector. With this instrument, structures can be projected and their images traced directly on drawing board. The scale of a stage micrometer can also be projected on each drawing, providing an easy method of scaling the structures drawn. The glossa was usually reconstructed in the drawings.

Results of Investigation

General Features of Ant Mouthparts

Detailed morphological investigations of ant mouthparts have appeared only occasionally. Bugnion (1924, 1925, 1930) produced the most extensive examinations of the mouthparts themselves; Janet (1899, 1904, 1905, 1911) exhaustively studied the musculature and segmentation of the ant head. Investigations including observations on the mouthparts of individual species or groups of species have provided much general information. Among others, Lubbock (1877), Forel (1874), Mukerji (1933), and Pavan and Ronchetti (1955), have produced studies of this nature. Wheeler (1910) and Forel (1928) give surprisingly brief descriptions of ant mouthparts in their general treatises, and both drew heavily from the works of Janet. In addition, the ant mouthparts, and the labium in particular, have never been clearly homologized with those of other Hymenoptera. As a result, it is important to present a clear description of the ant mouthparts and to review the terminology associated with these structures. As few as possible new terms are introduced here, and even these are presented only for the sake of convenience in this particular investigation. New terms are italicized when first introduced.

The mouthparts of insects comprise the labrum, the appendages of the gnathal segments, and the hypopharynx. The gnathal appendages are the mandibles, the first maxillae, and the second maxillae. The second maxillae are fused to form a labium (Snodgrass, 1928). A fundamental characteristic of the mouthparts of both larval and adult Hymenoptera is the lateral union of the maxillae with the labium to form a maxillo-labial complex (Matsuda, 1965). The maxillo-labial apparatus of the Tenthredinidae can be considered the basic hymenopteran type, since its structure is retained throughout the order with but "slight modifications" in most adult Hymenoptera (Snodgrass, 1935). Functioning as a single organ, the maxillo-labial complex of the higher Hymenoptera forms a channel along which food is passed to the mouth. In the ants, as in the other higher Hymenoptera, the maxillo-labial complex is suspended from the hypostomal bridge, which is formed from the medial union of the hypostomal lobes (figs. 12, 13). A medial union of the postgenae in the ants forms a much wider postgenal bridge behind and perhaps partially covering the hypostomal bridge. Two major openings are thus formed in the head capsule, the occipital foramen, and the oral foramen.

Labrum

In the ants the labrum is usually a broad, flaplike structure suspended from the lower edge of the clypeus (plates 1, 2). Although it has been characterized as being distinctly bilobed in the ants (Chatin, 1887), there are numerous exceptions to this generalization. A pair of adductor muscles are inserted on the labrum, but abductors are absent (Janet, 1899, 1905). There are no muscles within the labrum.

The labrum functions primarily in protecting the maxillo-labial complex, and together with the stipites it can effectively close off the buccal cavity from the environment (fig. 2). The labrum also often functions in holding food. In the dacetine ants the labrum functions in a locking mechanism which permits the mandibles to be passively held open in a spring-trap arrangement (Brown and Wilson, 1959).

The labrum is generally provided with abundant setae on its exterior face and distal margin, and usually the pattern of placement of the larger setae appears to be consistent within a species. A chaetotaxy of the labrum, however, has not been accomplished. The labral hemocoel is usually distinct in balsam preparations and is relatively constant in shape within species groups (fig. 4). The labrum itself assumes a wide range of shapes, many of which include a median cleft (fig. 4). In some species the labrum has one or more projections on its extensor surface or near its distal margin called *labral tubercles* (figs. 4, 5). They appear in a variety of shapes, from rounded and peglike to sharp and spinelike, and some of them serve to help hold active prey.

Mandibles

The articulation of the mandibles in the ants is dorsoventral, permitting the mandibles to move in one plane only, toward and away from the median longitudinal axis of the body (Matsuda, 1965). The mandible is provided with 2 muscles, an adductor and abductor (fig. 6). The adductor is voluminous and is the most prominent muscle within the head capsule. It is divided into several distinct fascicles and is inserted on the internal margin of the articulatory border of the mandible, by means of a large tendon. The much smaller abductor is ventral to the adductor and is inserted on the lower external margin of the articulatory border (Janet, 1905, 1911). There is no musculature within the mandibles. Marcus (1944, 1945) gives detailed descriptions of the mandibular musculature and articulation for several species of ants, and Barth (1960) describes the mandibular mechanism of *Odontomachus chelifer*. Brown and Wilson (1959b) have detailed the mandibular musculature and action of *Strumigenys ludia*.

The mandibles are usually provided with numerous setae in various arrangements and positions. Some arrangements are highly ordered along the masticatory margin of the mandible. Several xeric ant species, such as those belonging to the genus *Pogonomyrmex*, have on their mandibles and on the ventral surface of their heads, long, curved setae called psammophores or ammochaetae. These are used like baskets to carry sand and soil while excavating nests (Spangler and Rettenmeyer, 1966). A bizarre arrangement of unusual, heavy setae has been described for the ventral surfaces of the mandibles of *Tatuidris tatusia* (Brown and Kempf, 1967). These setae form a mandibular brush whose function has not yet been determined.

Janet (1904) described a series of sense organs on the mandibles and called these the *organes à ombelle*. No research has been performed on the sensitivity of these nor of the mandibular setae. The shape of the mandibles varies not only between species, but also frequently between the castes of a single species. The articulatory margins and the general configuration of the proximal end are relatively uniform throughout the Formicidae. Forel (1874) described the ant mandible in terms of the articulatory surface, external margin, internal margin, and terminal margin. The terms employed here are: the articulatory border, the external margin, the basal margin (= internal margin of Forel), the masticatory margin (= terminal margin of Forel), and the internal margin, comprising the basal and masticatory margins combined (fig. 6). These terms are not completely applicable to all mandibles (e.g., those of *Eciton* soldiers) and so are of limited value. Ettershank (1966) in his revision of a number of myrmicine genera introduced several new morphological terms for the mandible. Two of these are used here: the mandalus, a small unpigmented area at the base of the mandible on the dorsal surface; and the trulleum, a basin-shaped

depression, also on the dorsal surface, which runs near the parallel to the articulatory border (fig. 6). The distal-most tooth on the masticatory margin is the apical; the remaining teeth are called the subapicals.

Maxillae

The first maxilla is divided into the cardo, stipes, lacinia, galea, and maxillary palpus (figs. 2, 3, 7, 8, 12, 13).

Snodgrass (1928) calls the cardo a secondary subdivision of the base of the first maxilla. Crampton (1923) says that when the cardo is long, as in many of the higher Hymenoptera, it is usually directed outward or toward the lateral region of the body, and that a maxilla with such a cardo should be characterized as being exocardine. The cardo in the ants is relatively uniform throughout the family (fig. 7).

The stipes is broadly elongated and heavily sclerotized on its external surface (figs. 7, 8). It is broadly joined to the galea and lacinia on its internal surface by membrane, musculature, and by a supporting sclerite, which Bugnion (1930) called the epistipes (fig. 8). The distal end of the stipes bears the maxillary palpus; the proximal end bears a chitinized projection, originating on the dorsal surface, which provides an articulatory surface for the cardo. The lateral margin of the stipes is often sharply angled in its distal half. This angle, the *lateral shoulder*, is often provided with stout setae of unknown function (figs. 7, 8). The stipes sometimes bears a diagonal groove across the middle of its external surface, dividing it into two parts—the *distal external face* and the *proximal external face*. This *transverse stipital groove* accommodates the distal margin of the labrum when the maxillo-labial apparatus is withdrawn and the labrum pulled against it (figs. 2, 7, 8). The ventral and dorsal surfaces are both provided with setae. The maxillary palpi have a primitive number of 6 segments in the ants, but lesser numbers are common. The variation in palpal segmentation has been examined in detail by Borgmeier (1957) and Kusnezov (1951, 1954a, 1954b).

The galea and lacinia are so broadly joined as to seem almost like a continuous structure. Although the galea is larger than the lacinia, the latter structure is quite conspicuous in the ants. In many of the other higher Hymenoptera, the lacinia is greatly reduced (Crampton, 1923). Several terms are introduced here, since the galea and lacinia have rarely been examined in detail. The spatulate galea bears at its distal end a verrucose ridge, the *galeal crown*, which is provided with numerous long setae (fig. 7). Sometimes appearing near the free margin of the galea is a uniform row of large peglike setae called the *galeal comb* (fig. 7). On the internal surface of the galea is the maxillary comb, a series of regularly spaced, rigid setae (fig. 7). Forel (1874) illustrated the location of this comb on the galea, and Janet (1904) studied it in detail, describing the setae as being thick-walled and rigid and fixed in cylindrical fossae. He postulated that they were mechanoreceptors. This comb is basically uniform through-

out the Formicidae. Also on this surface are a series of small setae fixed in small cylindrical pits. These are located near the maxillary comb and were termed gustatory papillae by Forel (1874). Drawings of the galea are of the external surface (the surface exposed when the maxillo-labial apparatus is extended), but the maxillary comb has been added in each case as though the galea were transparent, which in fact it is on the microscope slide.

The lacinia is usually triangular and usually bears a row of setae along its free margin. These setae, the *lacinial comb*, can occur in a continuous or discontinuous array. The anterior triangular angle is the *gonia* and the posterior angle the *apex*. Few setae are found on the external or internal surfaces of the lacinia (figs. 7, 8, 12).

Inserted on the maxilla are 2 muscles, an adductor and an abductor. Several small muscles are located within the structure of the maxilla itself (Janet, 1905).

Labium, hypopharynx, epipharynx, and infrabuccal pocket

According to DuPorte (1967), the labium of insects consists of a postlabium which is adnate to the cranium and a prelabium which is free from the cranium. The postlabium is usually divided into a proximal submentum and a distal mentum; the prelabium includes the prementum, palpi, glossae, and paraglossae. Most entomologists have serially homologized the submentum of the labium with the cardines of the first maxillae, the mentum with the stipites, the glossa with the lacinia, and the paraglossae with the galea (Snodgrass, 1928). Some entomologists have considered the submentum and mentum to be derived from the sternum of the labial segment. Matsuda (1965) reported that the basal part of the maxillo-labial complex in the higher Hymenoptera does not develop in the same way as an independent appendage, and that the parts called the submentum, mentum, and prementum are not consecutive parts of a gnathal appendage. Snodgrass (1928) has reported that, like the cardines of the first maxillae, the submentum probably represents a secondary proximal subdivision of the second maxillae.

It is abundantly clear that the homologies and related terminology in the mouthparts of insects are far from being established and standardized. Earlier interpretations of the mouthparts of the higher Hymenoptera, including the ants, have called the large ventral sclerite of the labium the mentum and the small, proximal sclerite the submentum. This interpretation has been followed by Janet (1899, 1904, 1905, 1911), Kellogg (1902), Crampton (1923), Bugnion (1924, 1925, 1930), and Liu (1925). For *Iridomyrmex humilis*, Pavan and Ronchetti (1955) have called the large sclerite the postmentum and the smaller, proximal sclerite the prementum. Crampton (1928), for an unidentified ant, labeled the small sclerite the mentum but offered no explanation. He did not label the larger sclerite.

Matsuda (1965) reported that the prementum can be identified by the insertion of an extrinsic muscle on its proximal margin, and that in the higher Hymenoptera the prementum is often large. Using this definition, that area traditionally called the mentum becomes the prementum, and this designation is preferred here (fig. 9). The insertion of the extrinsic muscle (the labial abductor) has been figured by Janet (1905). The smaller sclerite traditionally called the submentum is arbitrarily referred to in the investigation as the postmentum (figs. 9, 10).

The prementum in ants is sclerotized on its ventral surface, forming a shieldlike plate, the *premental shield* (fig. 9). Sclerotization of this area varies in intensity throughout the ants. The prementum is usually provided with several long setae. The postmentum varies in shape but is most commonly triangular or U-shaped (fig. 10). The membranous dorsal surface of the prementum represents the hypopharynx which has completely fused with it (fig. 9). This is unlike the condition in more generalized pterygote insects, in which the hypopharynx hangs like a tongue in the preoral cavity (Snodgrass, 1928). In the Hymenoptera this hypopharyngeal lobe has been lost, and the salivary orifice serves as a marker for separating the hypopharyngeal region from the premental area of the labium. The duct of the salivary gland opens beneath the distal end of the hypopharynx (Matsuda, 1965).

The hypopharynx together with the epipharynx, a membranous wall beneath the labrum and clypeus, form a preoral food chamber — the cibarium, although in the ants this is not a clearly defined cavity. The hypopharynx and epipharynx have been discussed in detail by Bugnion (1925), who revealed his dismay at Savigny's (1816) original selection of these terms. They indicate that the structures are located above and below the pharynx, whereas in fact they are associated with the preoral cavity. Because of confusion surrounding the use of the term hypopharynx, Bugnion suggested that the term be abandoned. Bugnion (1924, 1925, 1930) has designated the shallow channel formed on the dorsal surface of the labium (actually the hypopharynx) as the labial groove (*gouttière labiale*) (figs. 11, 12).

A curved sclerite on each side of the labium at its proximal border acts to support the general structure of the labial-hypopharyngeal complex. These sclerites are inserted on the proximal lateral angles of the premental shield, pass dorsad along the side of the labium, then angle anteriorly and supposedly terminate in a rounded or triangulate expansion. The supporting sclerites have been called the "*baguettes de Huxley*" by Bugnion (1925), after Thomas Huxley who originally described these structures in *Bombus* (1878). Bugnion offered an alternative term for these, collectively calling them the epimentum. This term is preferred in this investigation, but has been modified to call these structures the *epimental sclerites* (fig.

9). For the terminal expansions of the epimental sclerites, Bugnion proposed the term "*raquettes*" (fig. 9). The epimental sclerites may be homologous with the ligular arms of the prementum of *Apis mellifera* (Matsuda, 1965).

The distal end of the labium is surmounted by the glossa, described by Matsuda (1965) as a protrusible tongue (figs. 9–13). The glossa is covered with a series of transverse ridges and laterally, near its base, is bounded by a row of sensory structures which have been described by Forel (1874) and Janet (1904). Forel supposed for them a gustatory function. The glossa is supported in part along its base by a sclerite which Bugnion (1924) called the sublingual plate. This plate is usually indistinct.

The paraglossae, a pair of lobelike structures that flank the glossa, are much reduced or absent in the ants. Bugnion (1925) reported that ants do not possess these structures, but Janet (1904) illustrated what appear to be paraglossae for *Myrmica rubra*, and Matsuda (1965) reported that in the ants the paraglossae are reduced and soft, and their paired nature is usually not recognizable. On each side of the labium, proximal to the glossa, is a set of large, rigid setae forming the *subglossal brushes* (figs. 9, 11). Called simply "*peignes*" by Forel (1874) and "*rateux*" by Bugnion (1924, 1930), many of the setae of these combs maintain the same diameter for most of their length, tapering only near their pointed ends, or in some cases widening at their ends and terminating bluntly.

The labial palpi are inserted near the distal lateral angles of the premental shield and have a primitive number of 4 segments in the ants, varying downwards to a single segment (figs. 3, 9, 11–13). The segmentation of these palpi is discussed in detail by Borgmeier (1947) and Kusnezov (1951, 1954a, 1954b).

Ants possess a chamber that is a diverticulum of the posterior hypopharynx called the infrabuccal pocket (fig. 11). Forel (1874) described this chamber as being filled with food particles, and Janet (1894, 1904, 1905) described the expelled contents of this pocket as the "*corpuscules de nettoyage*." Bugnion (1924, 1930) reported that the chamber served to agglutinate and shape into pellets the detritus arising from grooming and the solid fragments removed from food materials. Wheeler and Bailey (1920) presented a detailed historical review and a series of new observations on the pocket and its contents. They microscopically analyzed the composition of the infrabuccal pellets for numerous species. Eisner and Happ (1962) have indeed shown that the infrabuccal pocket is an effective filter device which renders crop-stored liquids relatively free from particles in at least some genera.

Inserted on the labium are a pair of adductor muscles and a pair of abductors. In addition, there are several muscles within the structure of the labium.

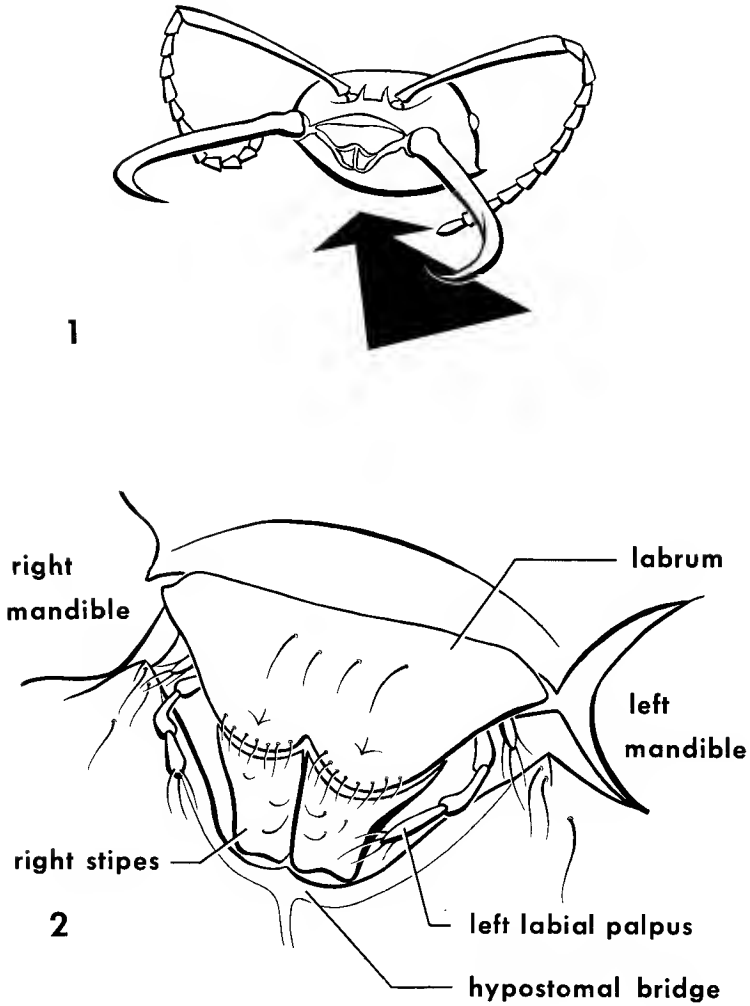


Plate 1. *Eciton mexicanum* (soldier).

Fig. 1. Anterior view of head, maxillo-labial apparatus retracted. Arrow indicates direction of view for figs. 2 and 3.

Fig. 2. Diagrammatic representation of mouthparts in situ, maxillo-labial apparatus retracted.

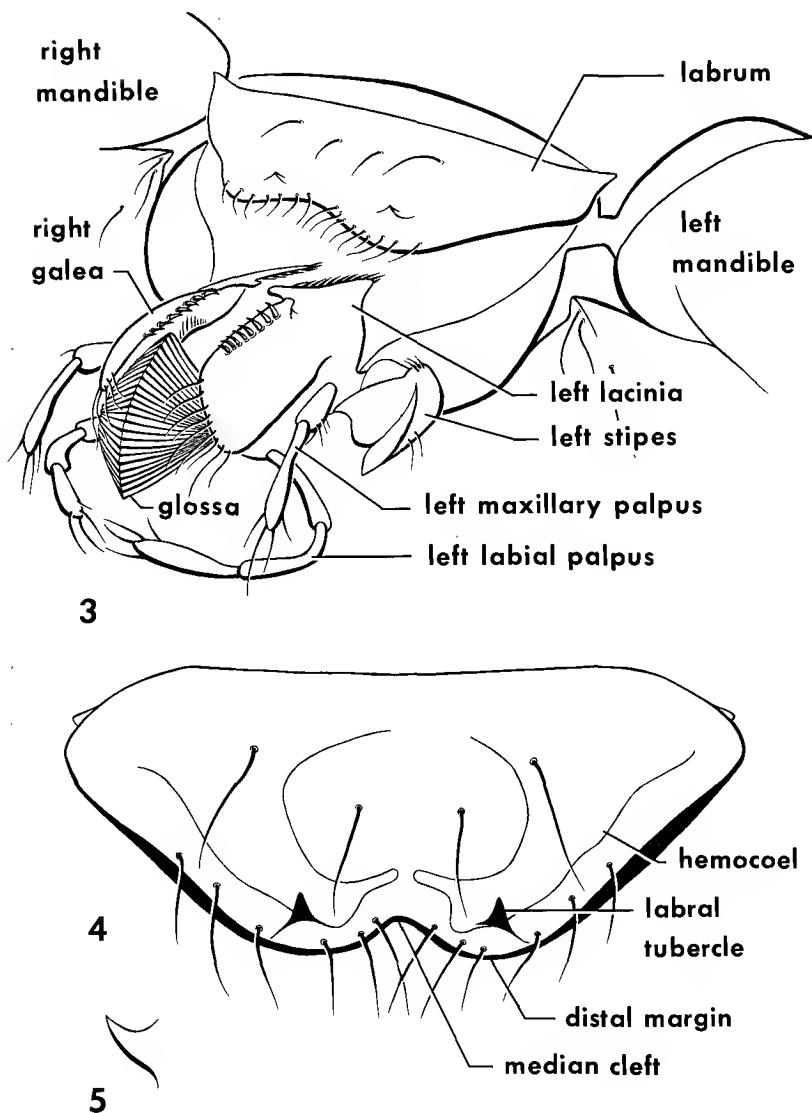
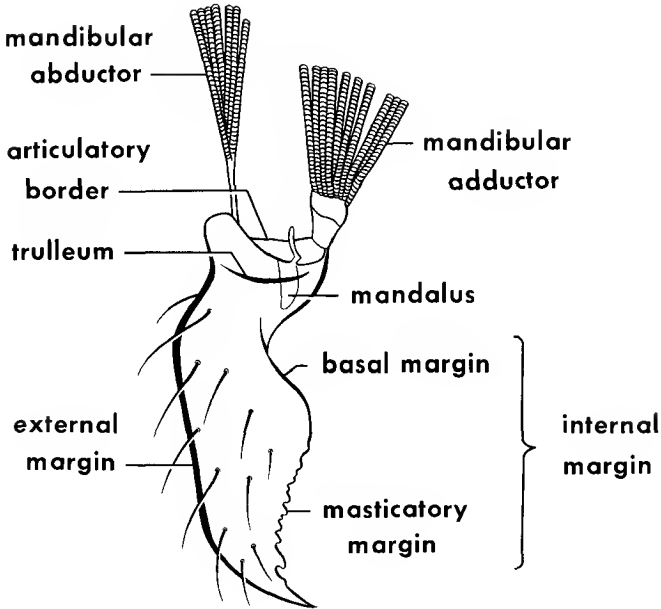


Plate 2. *Eciton mexicanum* (soldier).

Fig. 3. Diagrammatic representation of mouthparts in situ, maxillo-labial apparatus extended.

Fig. 4. Diagrammatic representation of labrum, external surface.

Fig. 5. Diagrammatic representation of labral tubercle, lateral view.



6

Plate 3. *Eciton mexicanum* (worker).

Fig. 6. Diagrammatic representation of right mandible, dorsal surface.

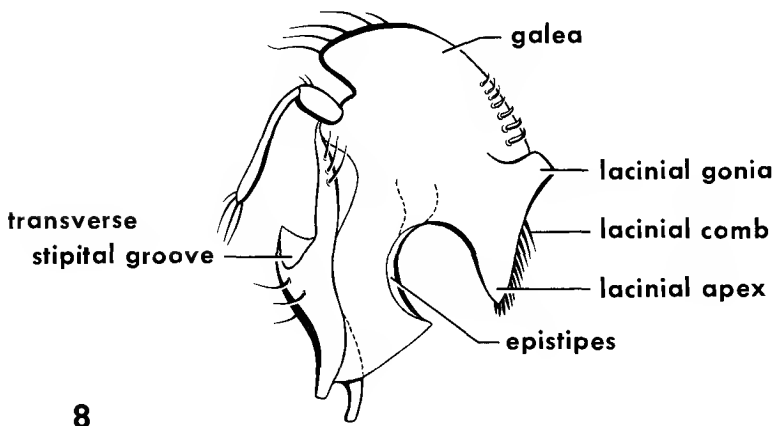
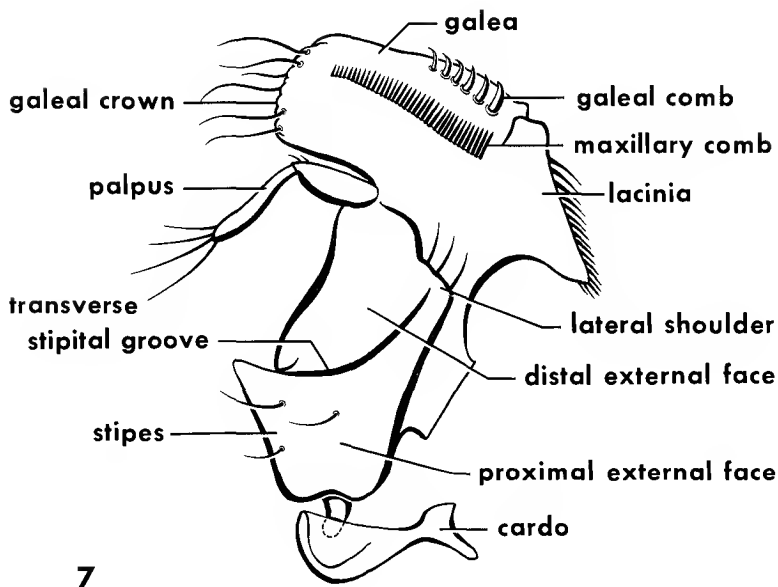


Plate 4. *Eciton mexicanum* (soldier).

Fig. 7. Diagrammatic representation of left maxilla as it appears flattened on microscope slide; view of external or exposed surfaces. Maxillary comb is on internal surface and is drawn as seen through transparent galea.

Fig. 8. Diagrammatic representation of left maxilla (without cardo) showing natural relationship of components.

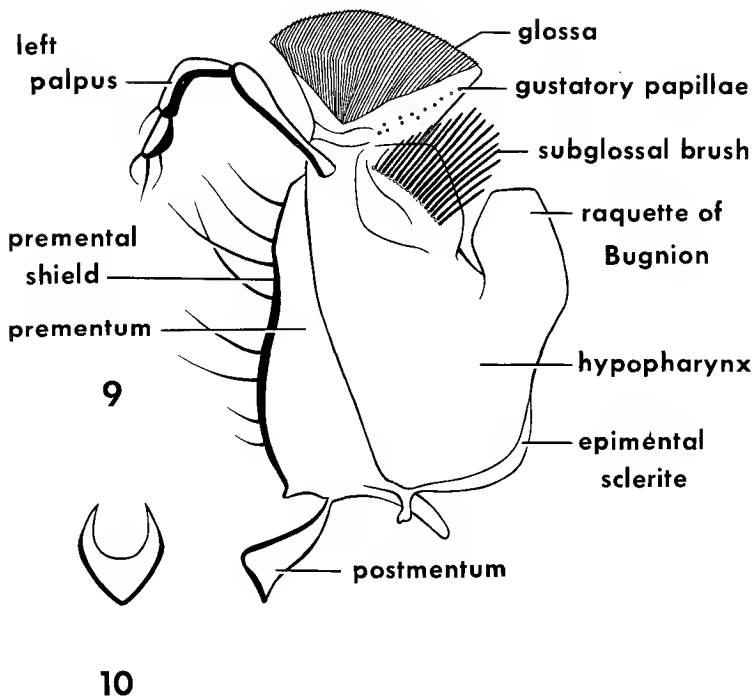
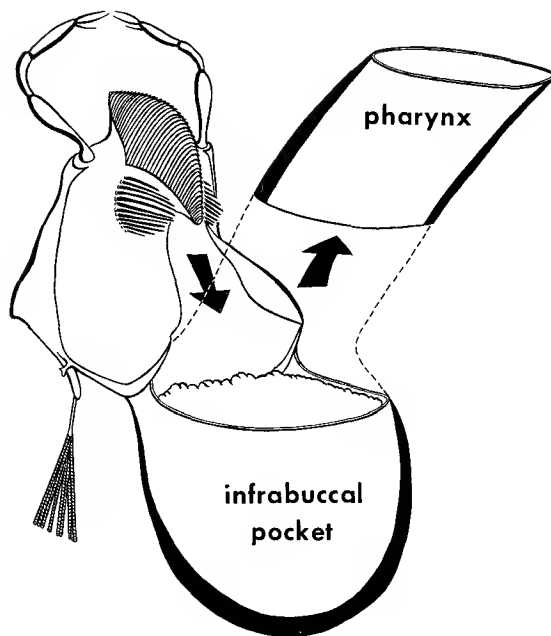


Plate 5. *Eciton quadriglume* (soldier).

Fig. 9. Diagrammatic representation of labium, lateral view.

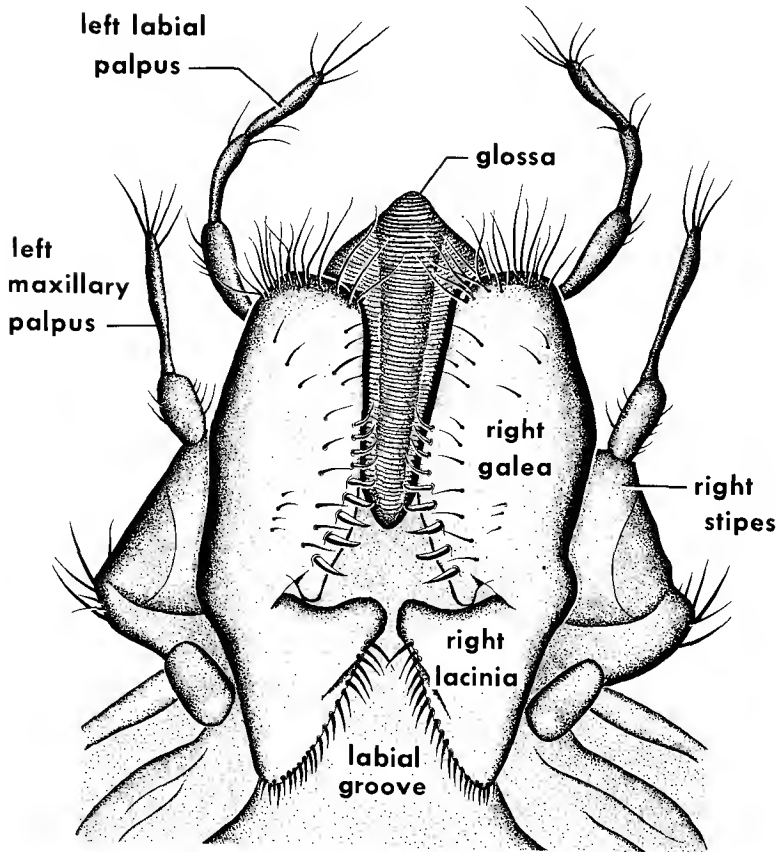
Fig. 10. Diagrammatic representation of postmentum, ventral view.



11

Plate 6. *Eciton mexicanum* (soldier).

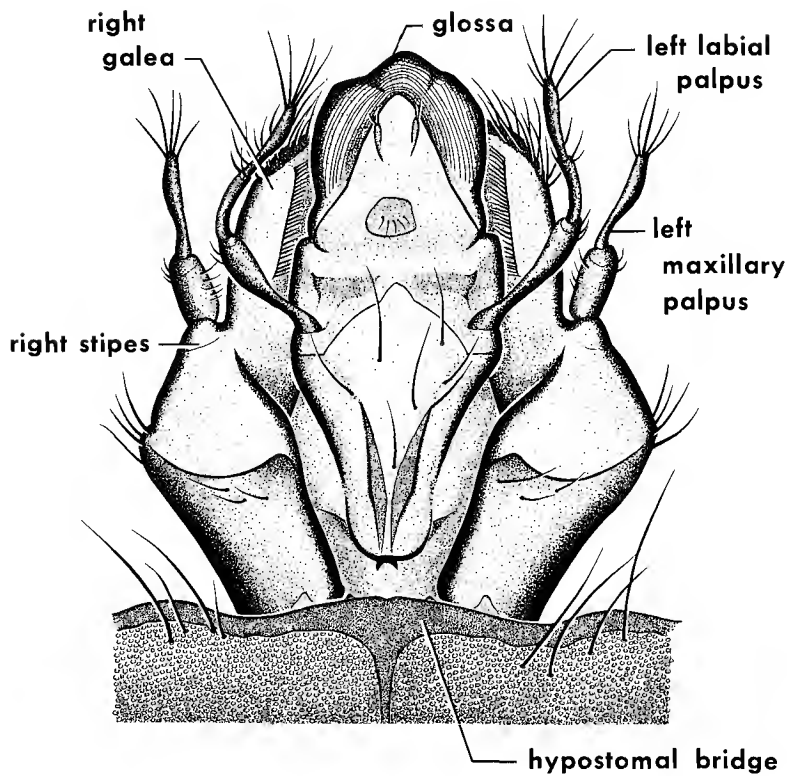
Fig. 11. Diagrammatic representation of labium, infrabuccal pocket, and pharynx. Arrows indicate path of materials along labial groove, past or into infrabuccal pocket, and through mouth into pharynx.



12

Plate 7. *Eciton mexicanum* (soldier).

Fig. 12. Mouthparts in situ, extended, dorsal view.



13

Plate 8. *Eciton mexicanum* (soldier).

Fig. 13. Mouthparts in situ, extended, ventral view.

Comparative Survey of Mouthparts of Representative Species

Most of the descriptions of mouthparts are accompanied by drawings of the individual trophic components. The labium has been omitted from many of the drawings. The glossa of the labium is often reconstructed, and the maxillary comb is drawn as seen through the transparent galea. The species of ants that were dissected are grouped under the subfamily designations recognized by Brown (1954). In the descriptions and illustrations, the species are arranged alphabetically by genus and species within their respective subfamilies.

Family Tiphidae

Subfamily Methochinae

Species examined:

Methocha stygia (female) (Plate 9)

Labrum (fig. 14). The labrum is not cleft, but is slightly emarginate at the center of its distal margin. Inserted slightly behind and along the distal margin is a row of long setae. The hemocoel almost fills the entire labrum.

Mandible (fig. 16). The masticatory and basal margins are not distinct from one another. An apical tooth and a subapical one are present; the trulleum and mandalus are absent.

Maxilla (figs. 17–19). The maxillary palpus is 6-segmented, and the stipes is without distinctive sculpture. The galea has a maxillary comb of 3 setae; the lacinia is without a distinct comb.

Labium (fig. 15). The labial palpus is 4-segmented. The premental shield is not clearly defined or heavily sclerotized, and extends laterally to cover the sides of the labium. The “lapping surface” of the glossa appears to be covered with rows of setae. Epimental sclerites are visible but not clearly defined, and they do not terminate in the expansive raquettes. Subglossal brushes are present and paraglossae are absent.

Subfamily Thynninae

Species examined:

Rhagigaster unicolor (female) (Plate 10)

Tachynomyia sp. (female) (Plate 11)

Labrum (figs. 23, 27). The labrum is narrowed posteriorly. Inserted near and along the length of the distal margin are 2 to 3 rows of setae, of which those of the proximal row are exceptionally long. The distal margin in *R. unicolor* is deeply emarginate medially. The hemocoel in *R. unicolor* consists of 2 arms, 1 extending into each lobe, and that of *Tachynomyia* consists of 1 arm that expands to fill the labrum.

Mandible (figs. 22, 25). The mandibles are considerably different in these 2 species. Those of *R. unicolor* are blunted apically and possess few setae, while those of *Tachynomyia* sp. are pointed apically and possess many long, thick setae on their ventral surfaces. In both species there is no distinction between the masticatory and basal margins, and there is no trulleum or mandalus.

Maxilla (figs. 21, 24, 28). The maxillary palpus of *R. unicolor* is 6-segmented; that of *Tachynomyia* is 3-segmented. Segments 1 and 2 of the palpus of *Tachynomyia* appear almost fused. The stipites differ in shape between the 2 species, and the stipites of *R. unicolor* has a longitudinal depression and ridge. Each species has a uniquely shaped cardo. The galea and lacinia differ in shape between the species, and the maxillary comb is absent in *Tachynomyia* sp.

Labium (figs. 20, 26). The labial palpus is 4-segmented; the premental shield in both species is poorly defined and extends laterally to cover the sides of the labium. Each species has subglossal brushes, although these are reduced in *Tachynomyia* sp. Paraglossae are absent.

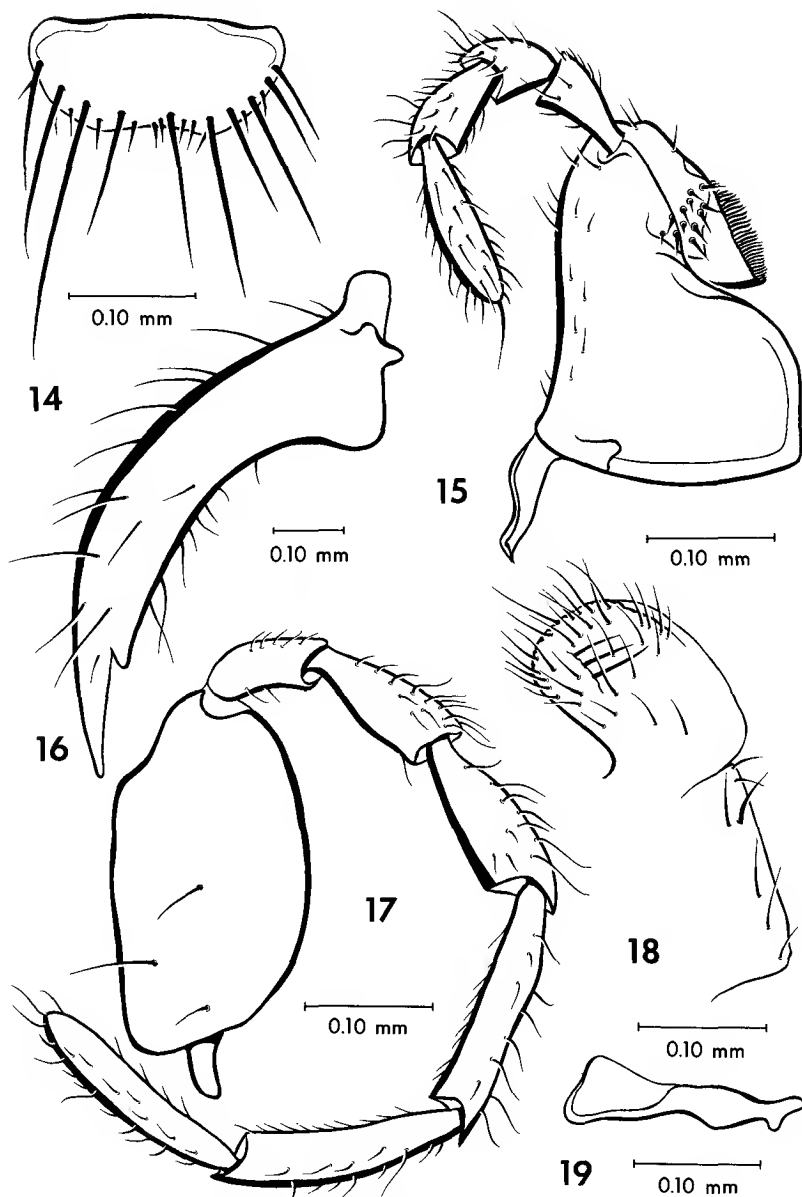


Plate 9. *Methocha stygia* (female).

- Fig. 14. Labrum, external view.
 Fig. 15. Labium with left labial palpus, lateral view.
 Fig. 16. Right mandible, dorsal view.
 Fig. 17. Left stipes and maxillary palpus, external view.
 Fig. 18. Left galea and lacinia, external view.
 Fig. 19. Left cardo, external view.

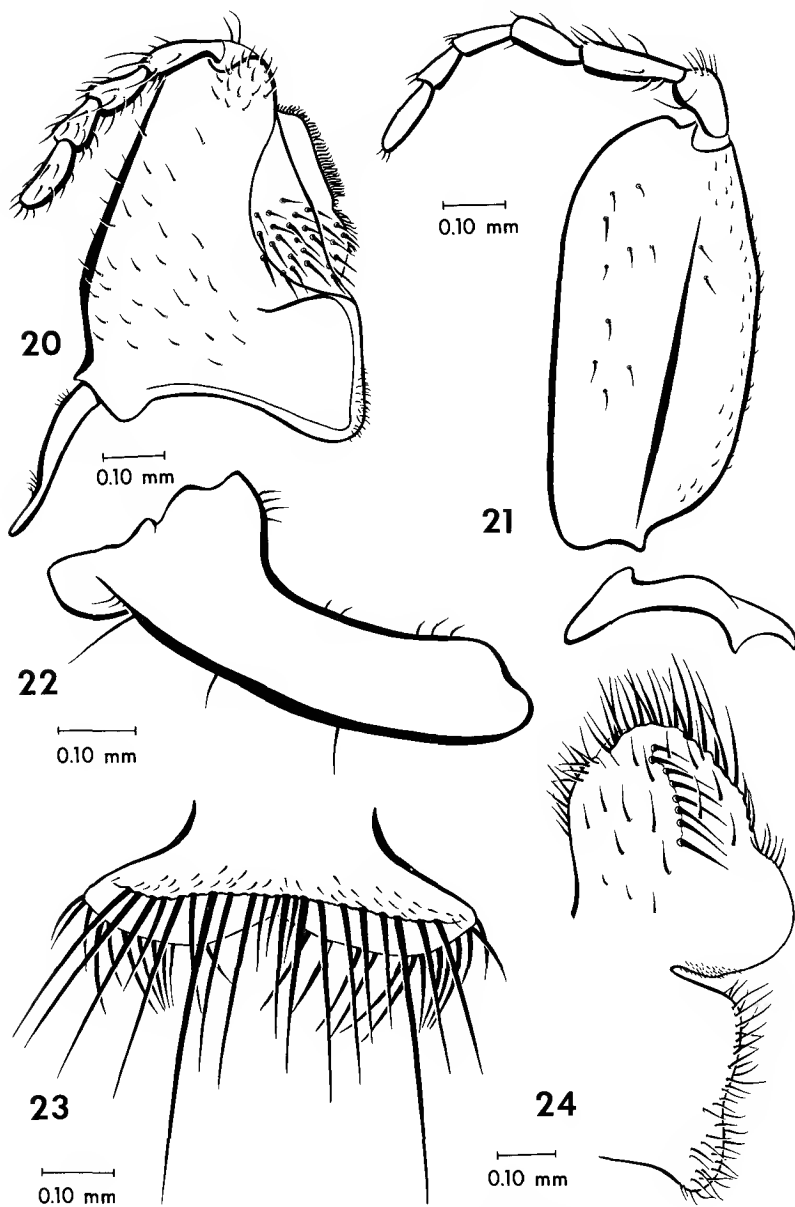


Plate 10. *Rhagigaster unicolor* (female).

- Fig. 20. Labium with left labial palpus, lateral view.
 Fig. 21. Left stipes maxillary palpus, and cardo, external view.
 Fig. 22. Right mandible, dorsal view.
 Fig. 23. Labrum, external view.
 Fig. 24. Left galea and lacinia, external view.

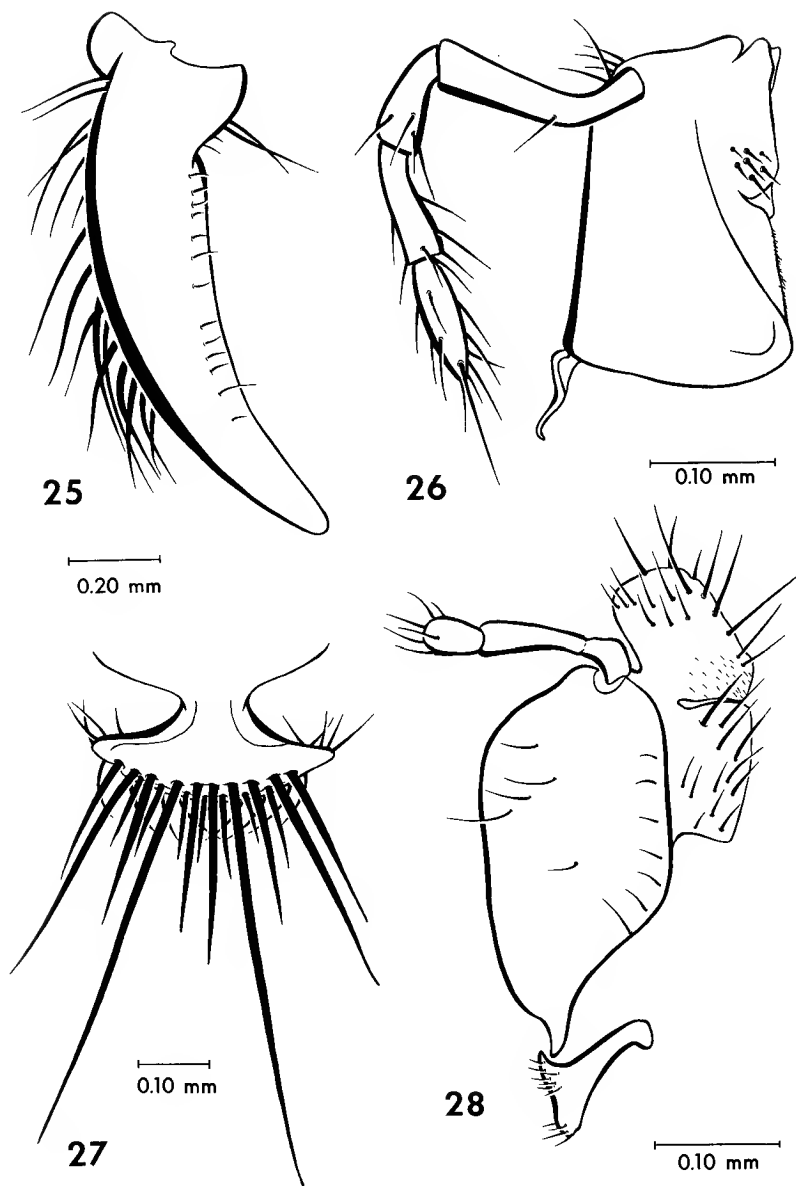


Plate 11. *Tachynomyia* sp. (female).

- Fig. 25. Right mandible, dorsal view.
Fig. 26. Labium with left labial palpus, lateral view.
Fig. 27. Labrum, external view.
Fig. 28. Left maxilla, external view.

Family Formicidae

Subfamily Ponerinae

Species examined:

Amblyopone pallipes (Plate 12)
Amblyopone n. sp.
Ectatomma tuberculatum
Gnamptogenys schubarti (Plate 13)
Hypoponera opacior (Plate 14)
Leptogenys group of *crassicornis*
 (Plate 15)
Megaponera foetens (Plate 16)
Myopias n. sp. in *maligna* group
 (Plate 17)
Odontomachus rixosus (Plate 18)

Pachycondyla crassinoda
Paraponera clavata (Plates 19, 20)
Platythyrea schultzei (Plate 21)
Ponera pennsylvanica (Plate 22)
Rhytidoponera turneri (Plate 23)
Simopelta oculata (Plate 24)
Termitopone commutata
 (Plates 25, 26)
Typhlomyrmex rogenhoferi
 (Plate 27)

Labrum. Most commonly the labrum of ponerines is cleft medially on the distal margin. This cleft is slitlike and, along with the customary emargination of the distal margin, divides the labrum into 2 lobes. In several genera, *Gnamptogenys* (fig. 38), *Paraponera* (fig. 64), *Platythyrea* (fig. 21) and *Typhlomyrmex* (fig. 94), the median cleft is absent. In these species the distal margin is generally emarginate. The hemocoel in the ponerine labrum consists of 2 arms, 1 extending into each lobe. These arms may or may not be united medially near the distal margin. Labral tubercles are absent (tubercles are present in some species of *Myopias* not examined here).

Mandible. The mandibles most commonly resemble those of *Megaponera foetens* (fig. 50), i.e., relatively generalized with distinct masticatory and basal margins. The masticatory margin is provided with numerous teeth. Several modifications of the mandible occur, the most extreme of these being in *Odontomachus* (fig. 60). Other modifications in shape and dentition occur in *Simopelta* (fig. 85), *Amblyopone* (fig. 32), *Myopias* (fig. 53) and *Leptogenys* (fig. 44). The trulleum and mandalus are always present, although not always conspicuous.

Maxilla. The maxillary palpus varies in the species examined from 1 segment in *Hypoponera opacior* (fig. 40) to 5 in *Paraponera clavata* (fig. 62); four segments is most common among the species. The stipites assume a variety of shapes, but commonly they resemble that of *Termitopone commutata* (fig. 90), in which the lateral margin is conspicuously curved outward. In most species 1 to 3 long setae are inserted at various locations on the proximal half of the stipes. These setae are not present in the 2 species of *Amblyopone* examined. A transverse stipital groove that accommodates the distal margin of the labrum is present in *Amblyopone* sp., *Rhytidoponera turneri* (fig. 79), *Gnamptogenys schubarti* (fig. 35), and *Typhlomyrmex rogenhoferi* (fig. 96). The stipes is often heavily sclerotized. The galea varies in shape from the long, narrow type of *Termitopone commutata* (fig. 88) to the shorter and broader type of *Simopelta oculata* (fig. 87). The galeal crown is flattened and bears a number of setae that may vary in thickness and shape, as can be seen in *Rhytidoponera turneri*

(fig. 80). A galeal comb is present in all species except *Hypoponera opacior*, *Leptogenys* sp. and *Simopelta oculata*. This comb may consist of a large number of short, stout setae, as in *Megaponera foetens* (fig. 52), or it may be reduced to a few such setae as in *Termitopone commutata* (fig. 88). The galeal comb of *Rhytidoponera turneri* (fig. 80) comprises more than 15 small setae, and may not be homologous with other ponerine galeal combs. The lacinia is usually triangular, as in *Odontomachus rixosus* (fig. 61), but may be rounded as in *Rhytidoponera turneri* (fig. 80). The lacinial comb is nearly always conspicuous and continuous. The lacinial gonia often bears one or more stout setae — found in *Gnamptogenys* (fig. 34), *Leptogenys* (fig. 45), *Megaponera* (fig. 52), *Myopias* (fig. 57), *Odontomachus* (fig. 61), *Ponera* (fig. 73), and *Termitopone* (fig. 88).

Labium. The labial palpus varies in number of segments from 2 to 4. The premental shield is often heavily sclerotized as in *Paraponera clavata* (figs. 66, 67), and commonly bears several large setae. Its lateral margins are not clearly defined as the shield becomes membranous laterally. In some species such as *Simopelta oculata* (fig. 83), the premental shield is not heavily sclerotized. The proximal lateral angles of the prementum are elongated, forming 2 armlike structures, each of which articulates with an epimental sclerite. These sclerites are never clearly defined since they also are membranous in part. In no species do the distal ends of the epimental sclerites expand to form “*raquettes*,” not, at least, any such as described by Bugnion (1925). Subglossal brushes are always present. The setae of these brushes are usually tapered throughout their length and terminate in a point; however, in some species (e.g. *Amblyopone pallipes*) the setae are expanded and rounded terminally (fig. 29). If the labium is viewed laterally, portions of the subglossal brush are usually hidden from view by folds of membrane that form the sides of the labium. The glossa is rarely preserved in its natural form, as has been indicated previously, and thus it is difficult to ascertain this structure's position and shape in the various species. This structure was well preserved in specimens of *Amblyopone pallipes* and *Odontomachus rixosus* (see figs. 29, 58). The most intriguing structures in some species are the paired paraglossae and/or paraglossal sensory pegs. Whether these lobelike structures, one on each side of the labium at the base of the glossa, are homologous with the paraglossae of other Hymenoptera is not known. Such structures were found in *Amblyopone pallipes* (fig. 29), *A.* sp., *Hypoponera opacior*, *Odontomachus rixosus* (figs. 58, 333), *Paraponera clavata* (fig. 67) and *Ponera pennsylvanica*. Of these, *Hypoponera opacior*, *Odontomachus rixosus*, and *Ponera pennsylvanica* possessed 1 or 2 sensory pegs on the paraglossae. The paraglossae (with 2 sensory pegs) of *Odontomachus rixosus* are most highly developed (fig. 333). Even in the absence of paraglossal lobes, several species have sensory pegs (1–3) about where lobes are found in other species. Species with just pegs are *Gnamptogenys schubarti* (1 peg per side), *Megaponera foetens* (3 pegs), *Myopias* sp. (3 pegs), *Pachycondyla crassinoda* (3 pegs), *Rhytidoponera turneri* (1 peg), *Termitopone commutata* (2 pegs), and *Typhlomyrmex rogenhoferi* (1 peg).

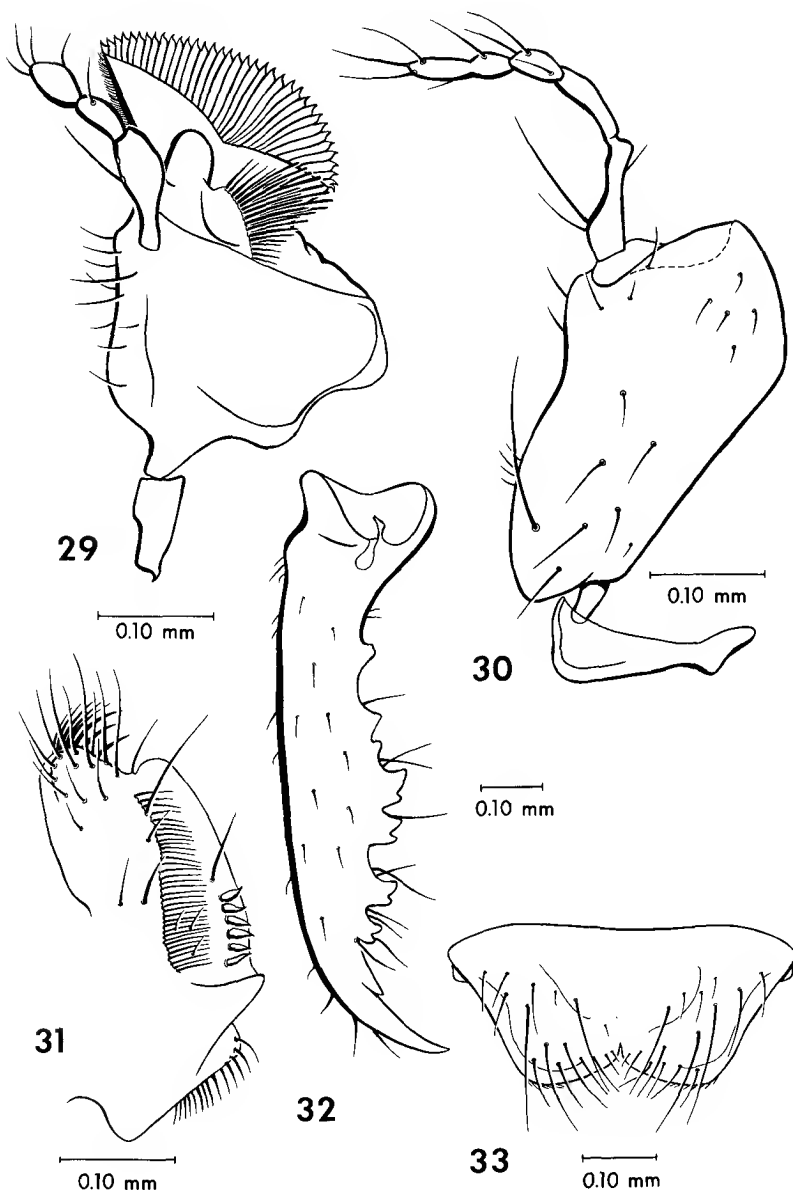


Plate 12. *Amblyopone pallipes* (worker).

- Fig. 29. Labium with left labial palpus, lateral view.
 Fig. 30. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 31. Left galea and lacinia, external view.
 Fig. 32. Right mandible, dorsal view.
 Fig. 33. Labrum, external view.

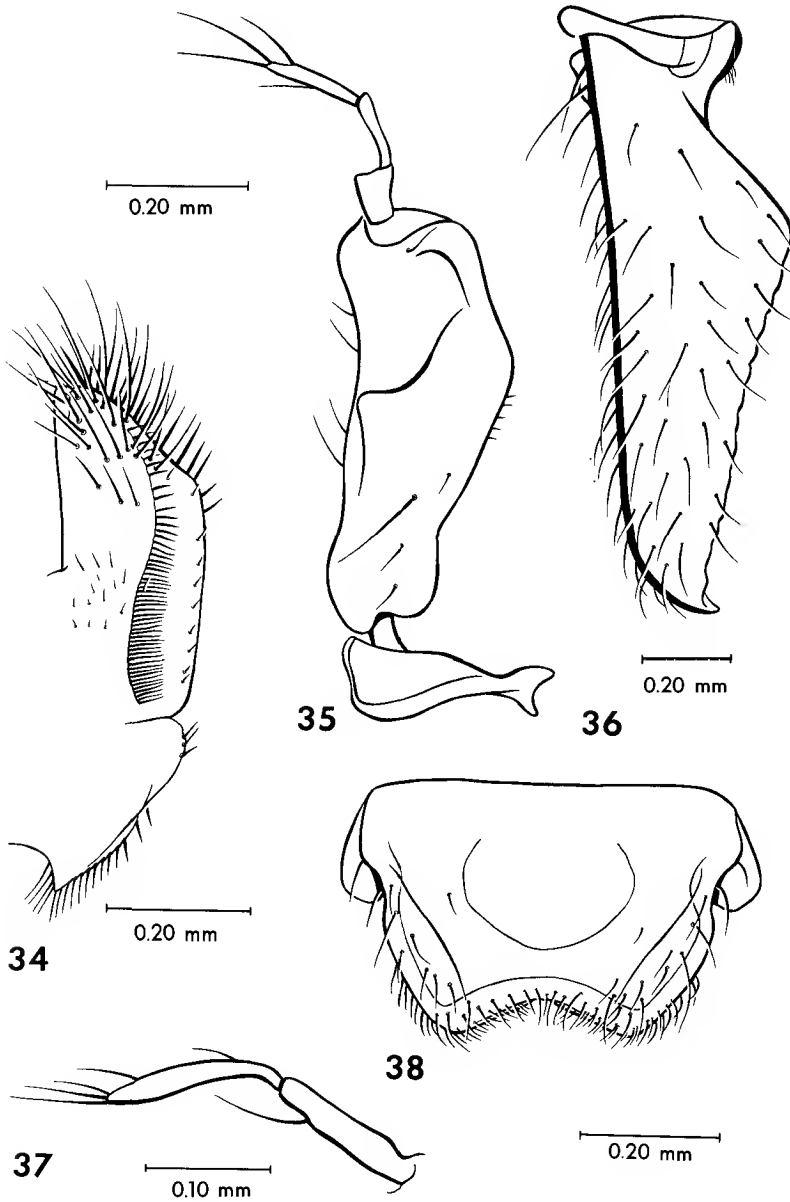


Plate 13. *Gnampptogenys schubarti* (worker).

- Fig. 34. Left galea and lacinia, external view.
 Fig. 35. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 36. Right mandible, dorsal view.
 Fig. 37. Left labial palpus, lateral view.
 Fig. 38. Labrum, external view.

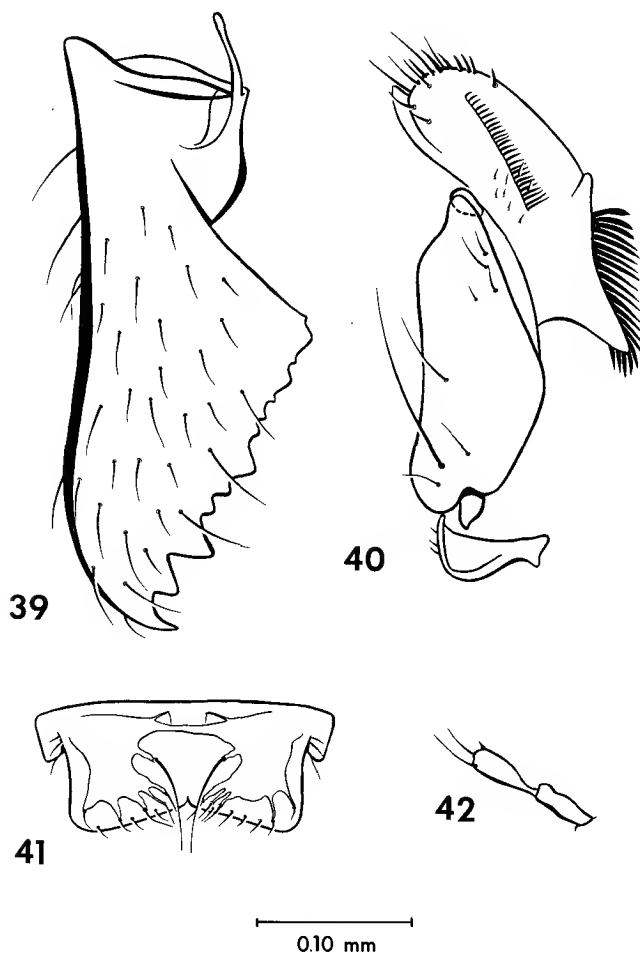


Plate 14. *Hypoponera opacior* (worker).

Fig. 39. Right mandible, dorsal view.

Fig. 40. Left maxilla, external view.

Fig. 41. Labrum, external view.

Fig. 42. Left labial palpus, lateral view.

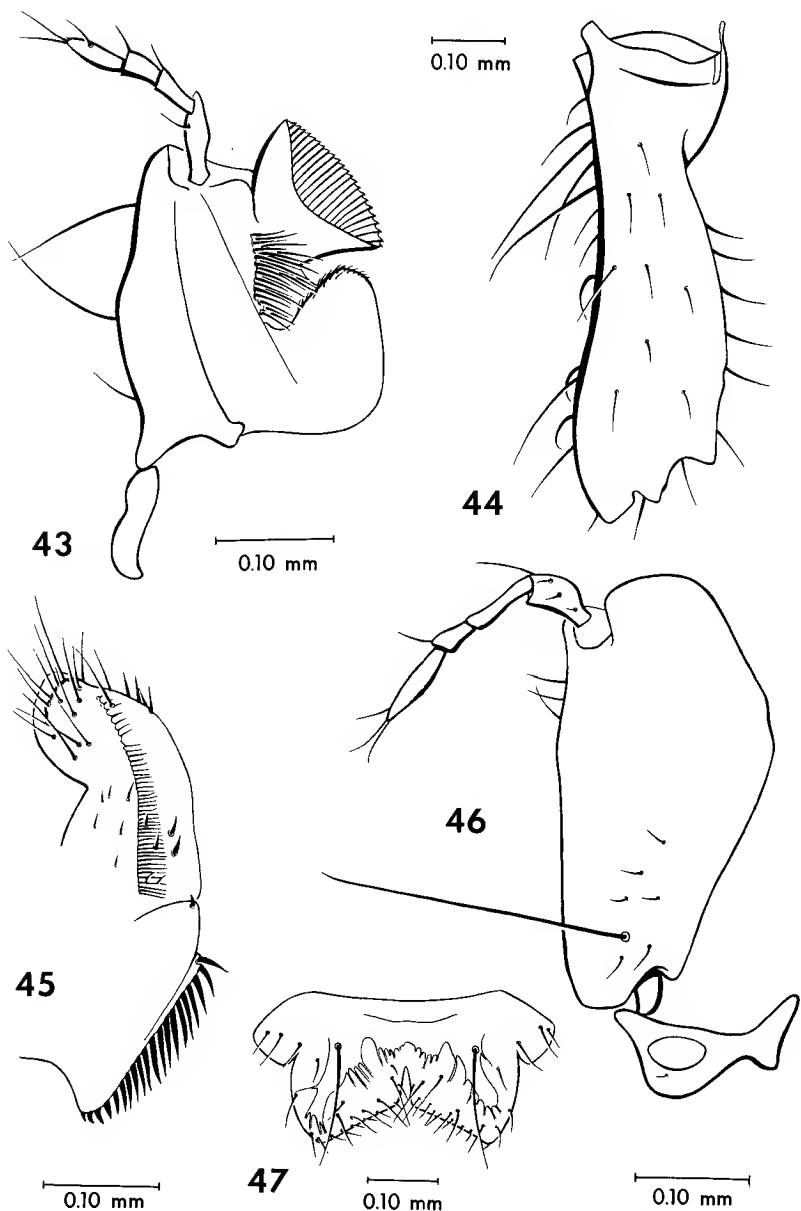


Plate 15. *Leptogenys* group of *crassicornis* (worker).

- Fig. 43. Labium with left labial palpus, lateral view.
 Fig. 44. Right mandible, dorsal view.
 Fig. 45. Left galea and lacinia, external view.
 Fig. 46. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 47. Labrum, external view.

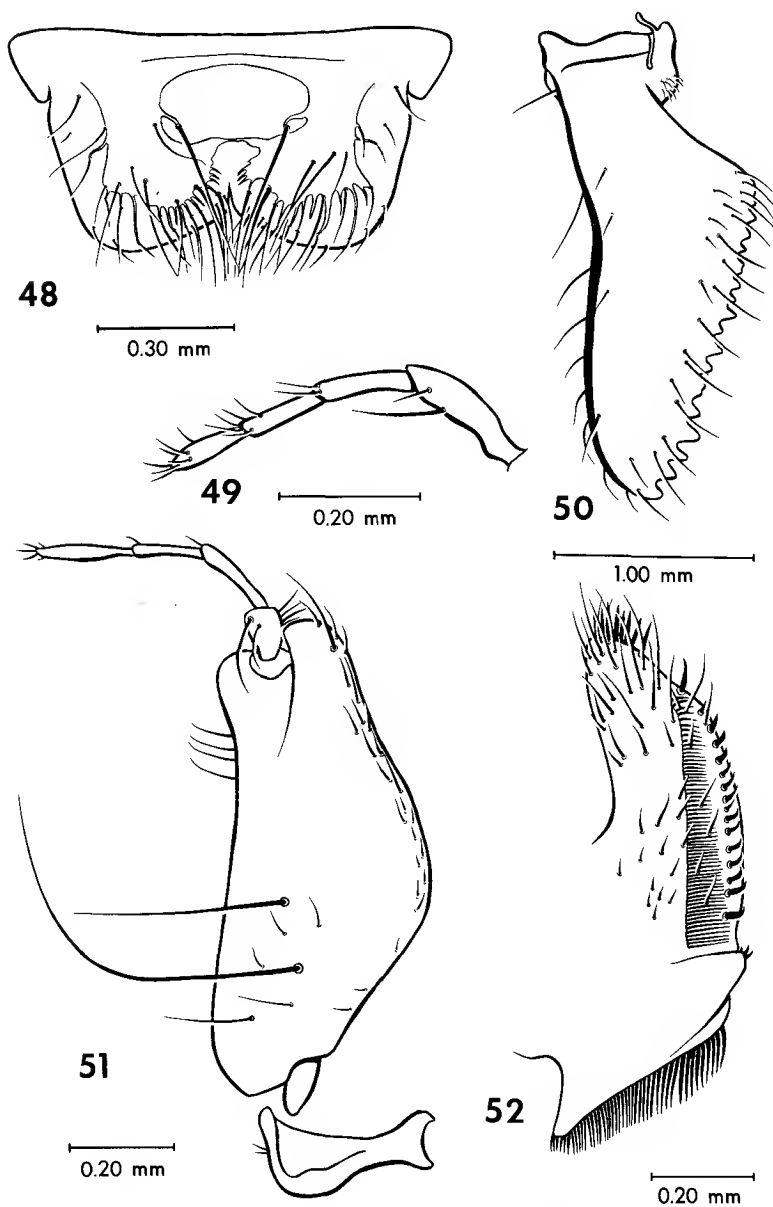


Plate 16. *Megaponera foetens* (worker).

- Fig. 48. Labrum, external view.
 Fig. 49. Left labial palpus, lateral view.
 Fig. 50. Right mandible, dorsal view.
 Fig. 51. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 52. Left galea and lacinia, external view.

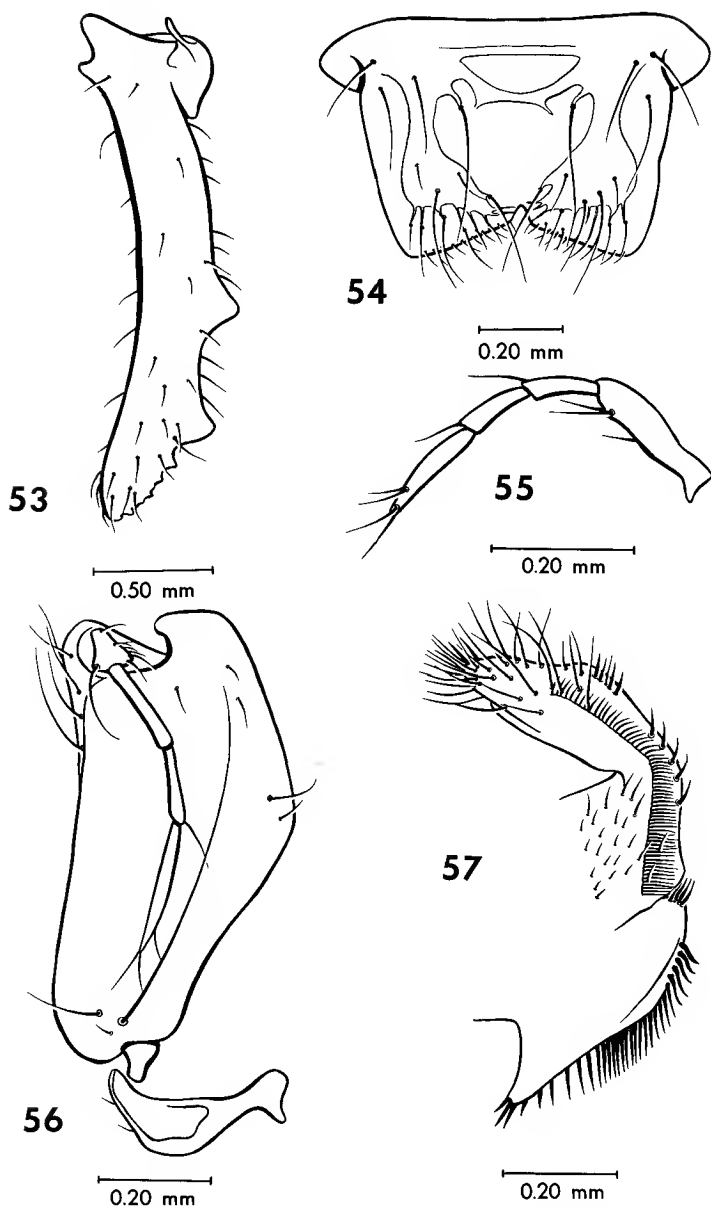


Plate 17. *Myopias* n.sp. in *maligna* group (worker).

- Fig. 53. Right mandible, dorsal view.
 Fig. 54. Labrum, external view.
 Fig. 55. Left labial palpus, lateral view.
 Fig. 56. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 57. Left galea and lacinia, external view.

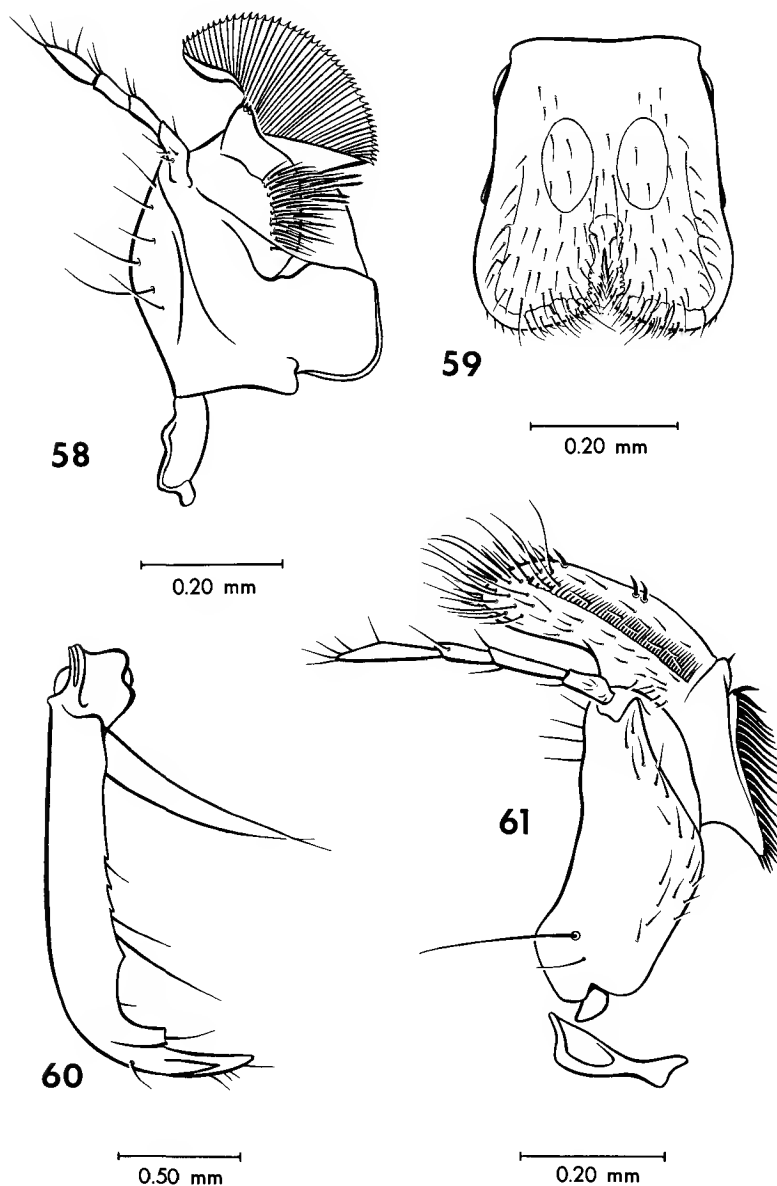


Plate 18. *Odontomachus rixosus* (worker).

Fig. 58. Labium with left labial palpus, lateral view.

Fig. 59. Labrum, external view.

Fig. 60. Right mandible, dorsal view.

Fig. 61. Left maxilla, external view.

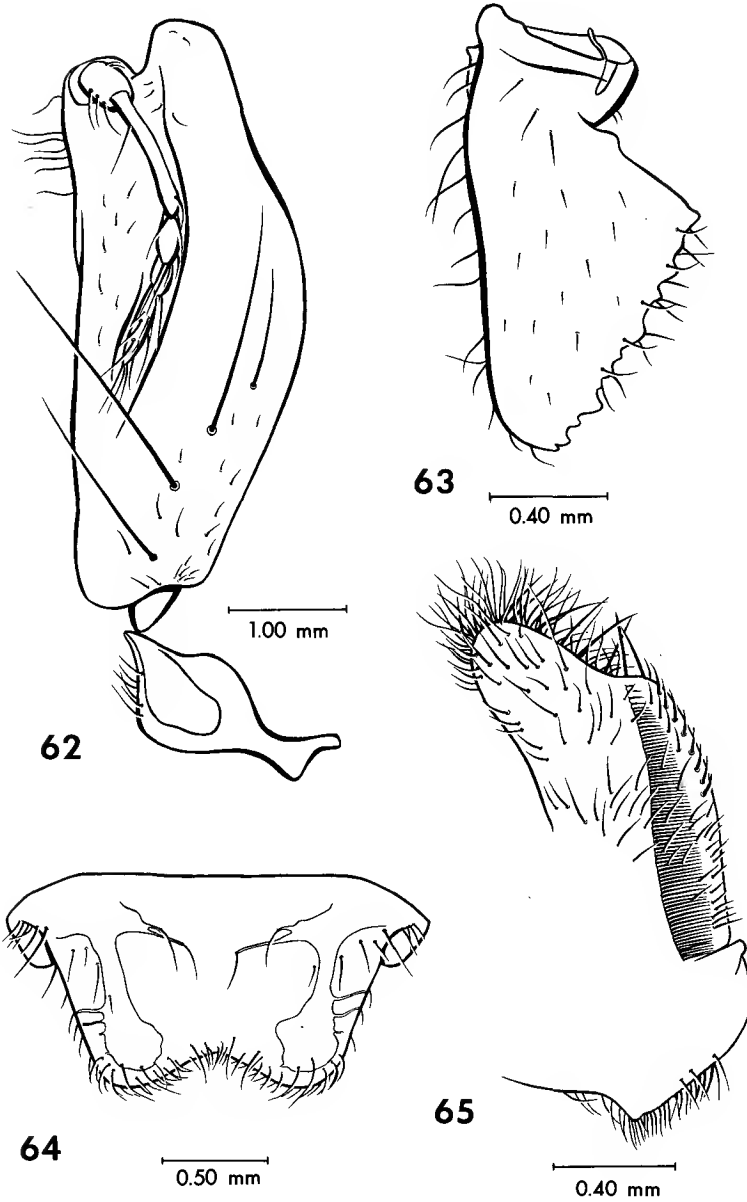


Plate 19. *Paraponera clavata* (worker).

- Fig. 62. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 63. Right mandible, dorsal view.
 Fig. 64. Labrum, external view.
 Fig. 65. Left galea and lacinia, external view.

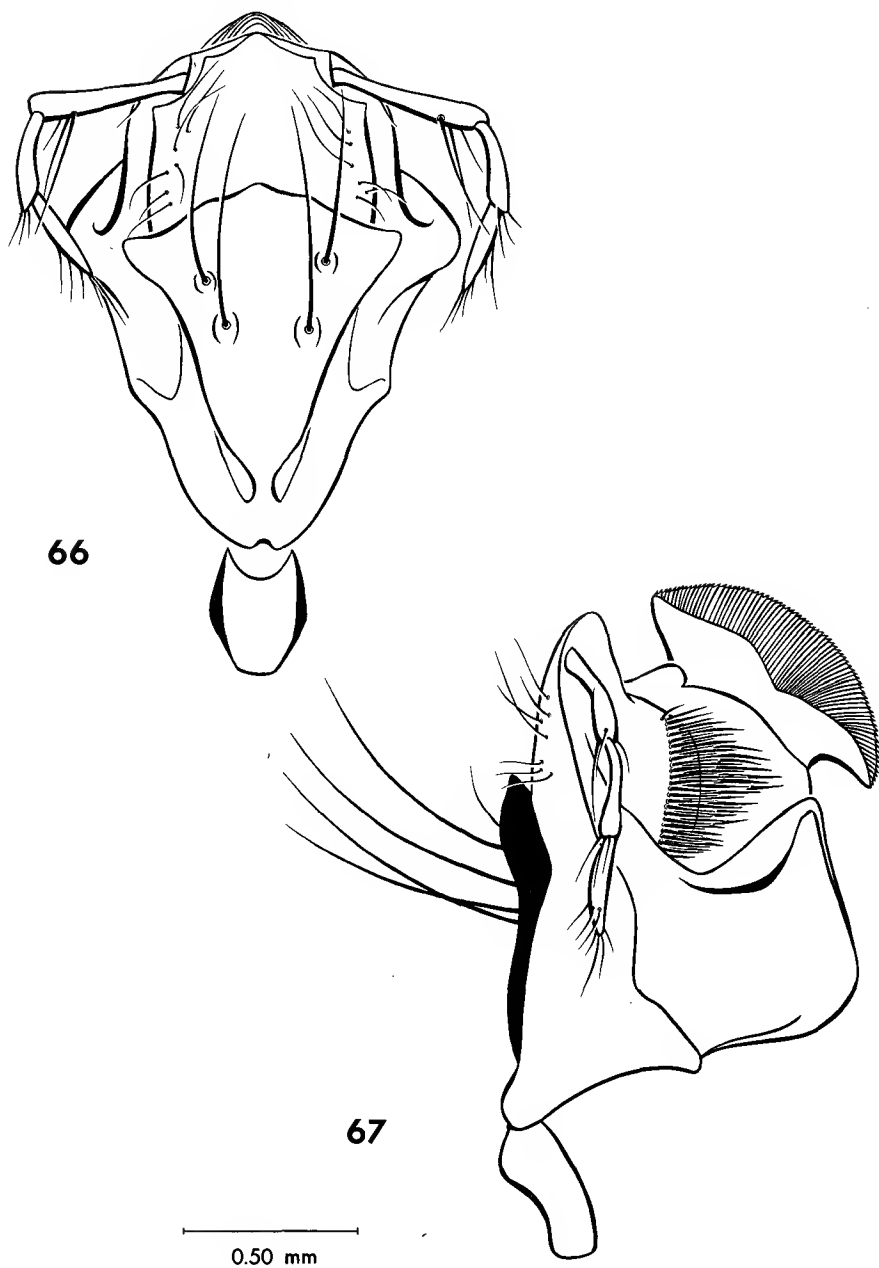


Plate 20. *Paraponera clavata* (worker).

Fig. 66. Labium, ventral view.

Fig. 67. Labium, lateral view.

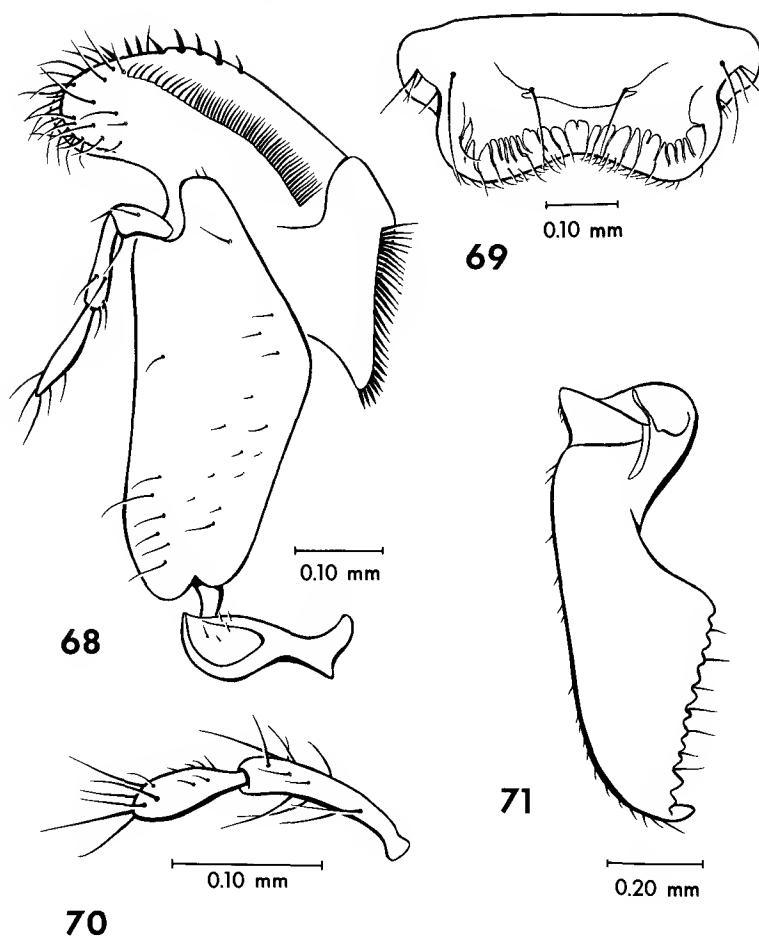


Plate 21. *Platythyreia schultzei* (worker).

Fig. 68. Left maxilla, external view.

Fig. 69. Labrum, external view.

Fig. 70. Left labial palpus, lateral view.

Fig. 71. Right mandible, dorsal view.

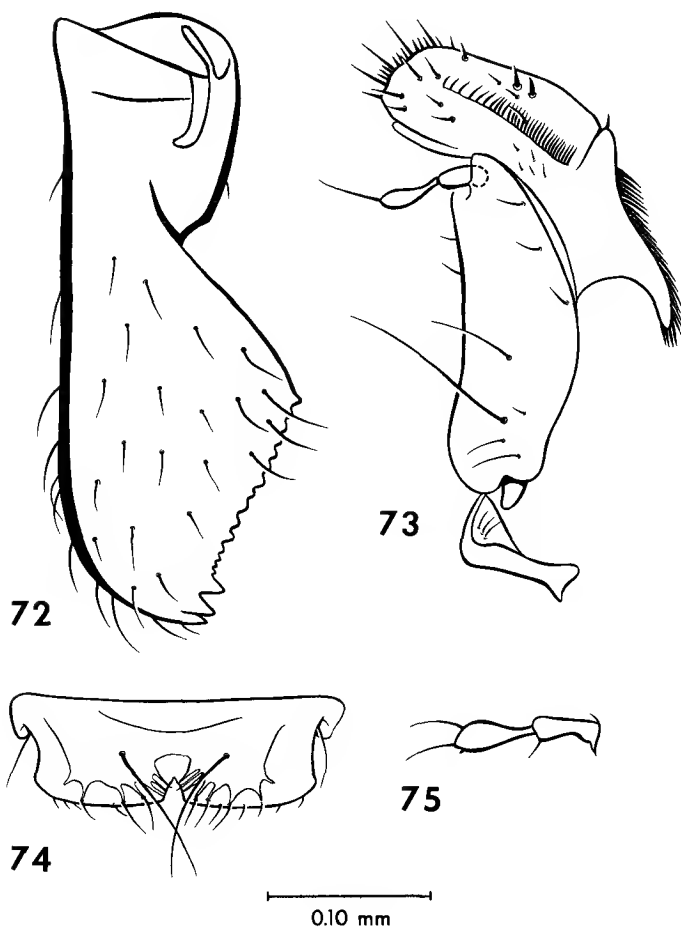


Plate 22. *Ponera pennsylvanica* (worker).

Fig. 72. Right mandible, dorsal view.

Fig. 73. Left maxilla, external view.

Fig. 74. Labrum, external view.

Fig. 75. Left labial palpus, lateral view.

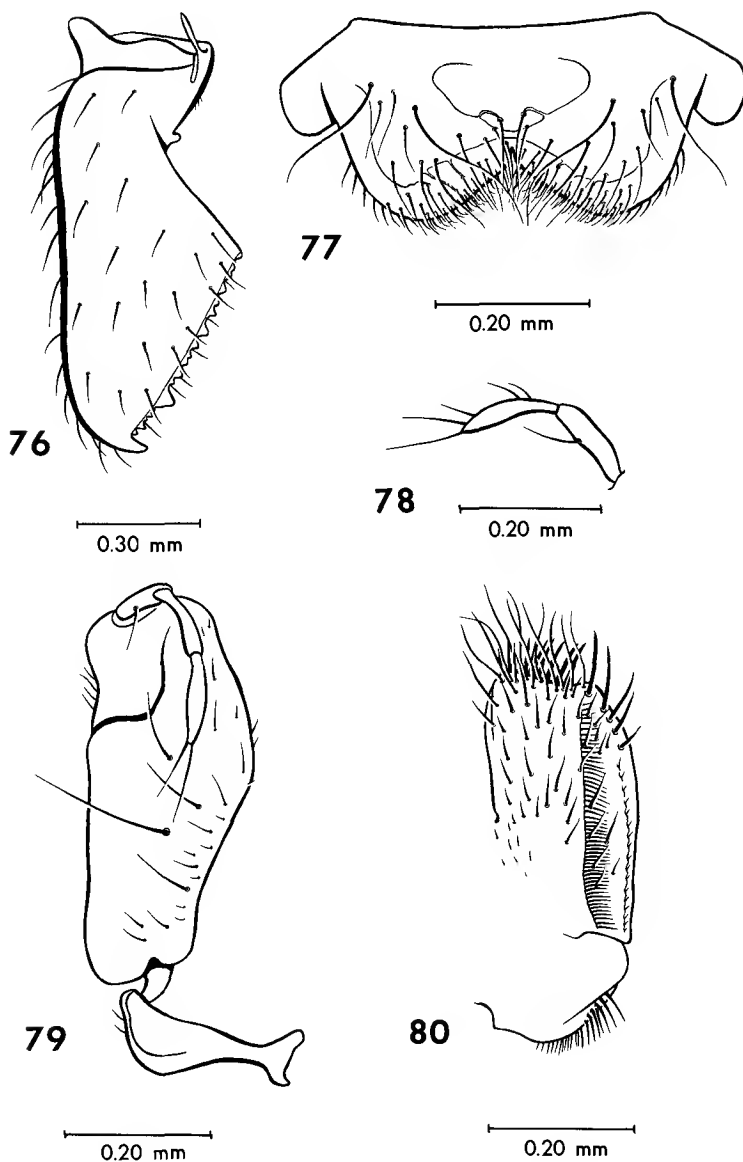
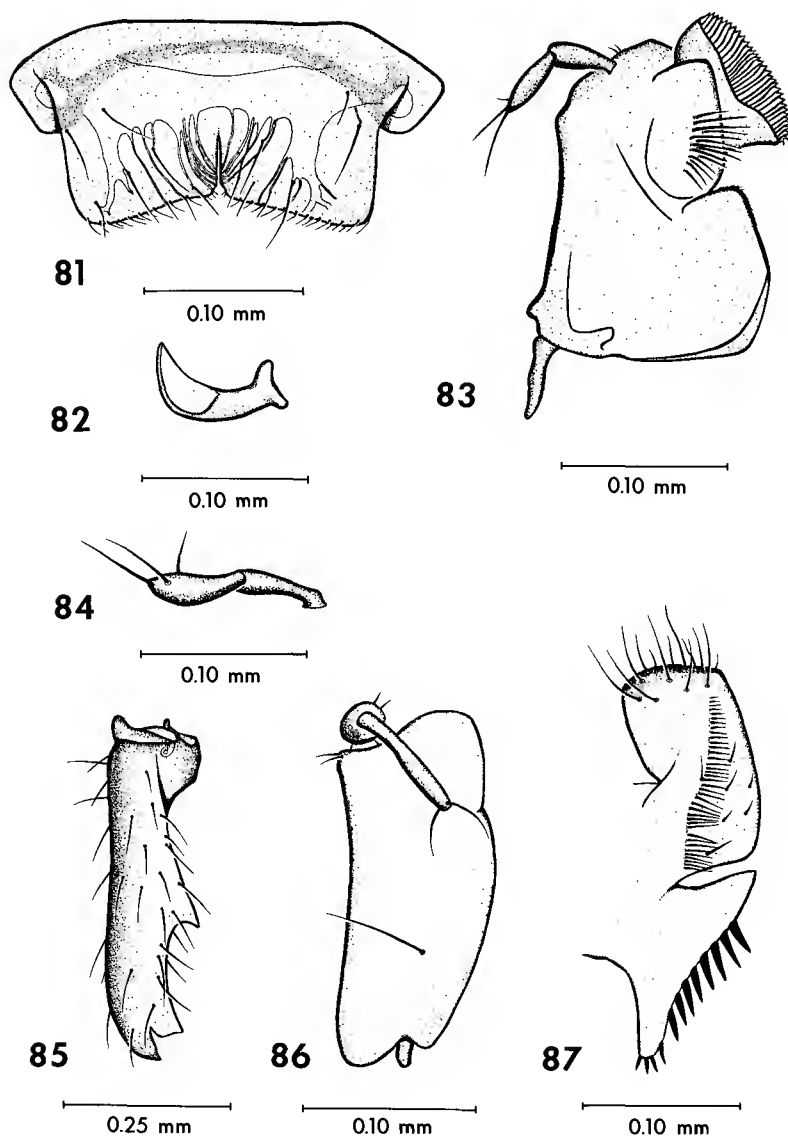


Plate 23. *Rhytidoponera turneri* (worker).

- Fig. 76. Right mandible, dorsal view.
Fig. 77. Labrum, external view.
Fig. 78. Left labial palpus, lateral view.
Fig. 79. Left stipes, maxillary palpus, and cardo, external view.
Fig. 80. Left galea and lacinia, external view.

Plate 24. *Simopelta oculata* (worker).

- Fig. 81. Labrum, external view.
 Fig. 82. Left cardo, external view.
 Fig. 83. Labium with left labial palpus, lateral view.
 Fig. 84. Left labial palpus, lateral view.
 Fig. 85. Right mandible, dorsal view.
 Fig. 86. Left stipes, external view.
 Fig. 87. Left galea and lacinia, external view.

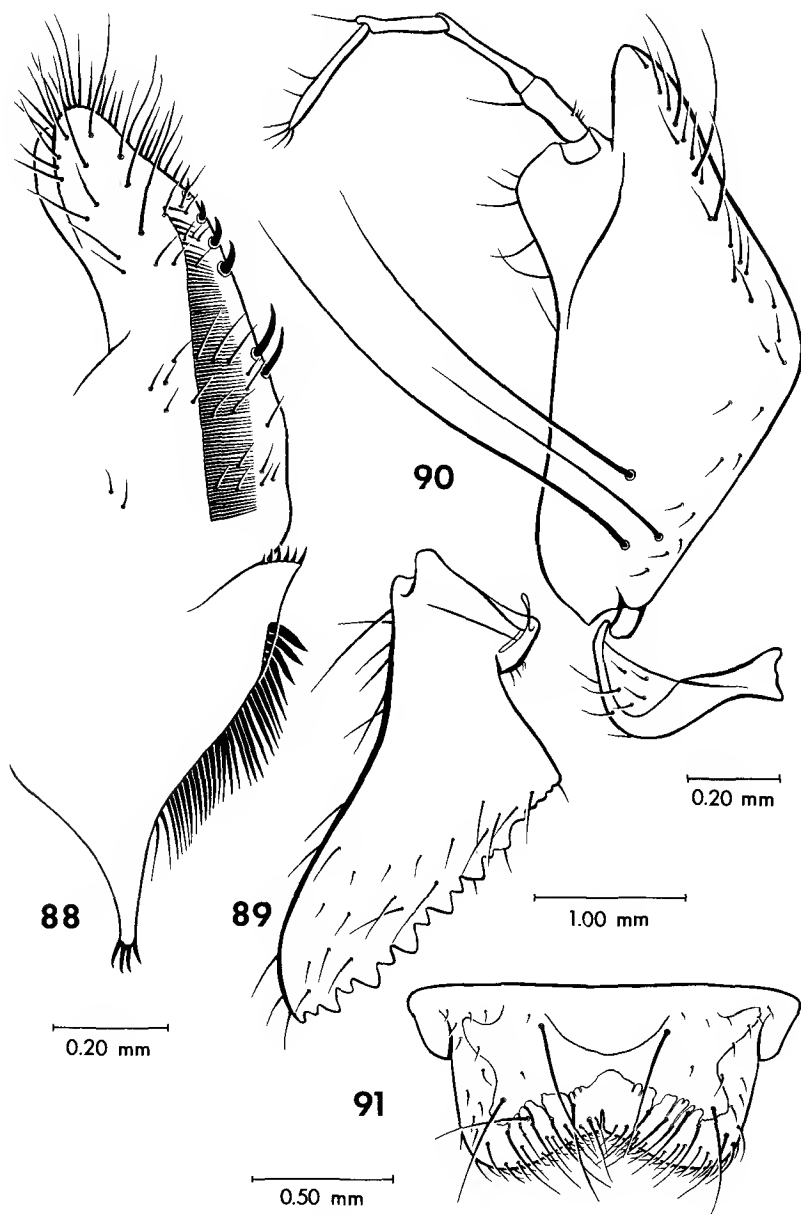


Plate 25. *Termitopone commutata* (worker).

Fig. 88. Left galea and lacinia, external view.

Fig. 89. Right mandible, dorsal view.

Fig. 90. Left stipes, maxillary palpus, and cardo, external view.

Fig. 91. Labrum, external view.



92

0.20 mm

Plate 26. *Termitopone commutata* (worker).

Fig. 92. Labium with left labial palpus, lateral view.

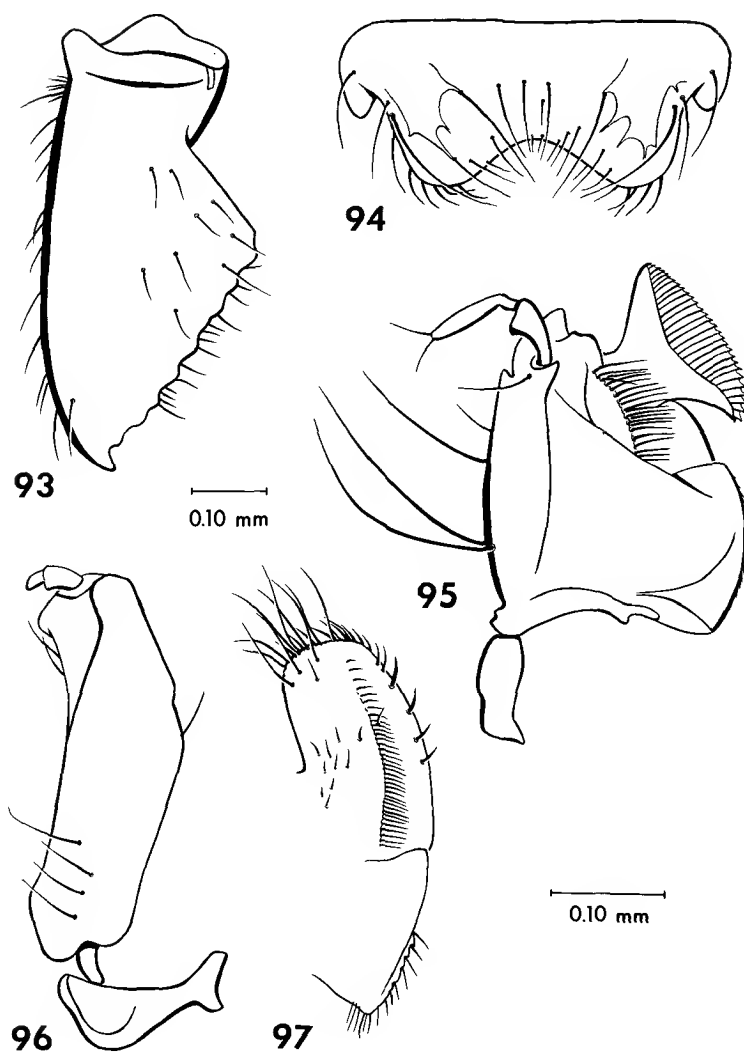


Plate 27. *Typhlomyrmex rogenhoferi* (worker).

Fig. 93. Right mandible, dorsal view.

Fig. 94. Labrum, external view.

Fig. 95. Labium with left palpus.

Fig. 96. Left stipes, maxillary palpus, and cardo, external view.

Fig. 97. Left galea and lacinia, external view.

Subfamily Cerapachyinae

Species examined:

Acanthostichus sp. near *quadratus* (Plate 28)

Cerapachys opaca (Plate 29)

Cerapachys sp. (Plate 30)

Cylindromyrmex striatus (Plate 31)

Sphinctomyrmex steinheili (Plate 32)

Labrum. The labrum is cleft medially, dividing it into 2 lobes, except in *Cylindromyrmex* (fig. 115), where it is only slightly emarginate medially. The labrum is basically the same shape among the species examined, except for *Acanthostichus* sp. (fig. 102), in which it is much longer in proportion to its width, and for *Cylindromyrmex* (fig. 115) in which it is not bilobed. The hemocoel consists of two arms, one entering each of the lobes. These arms are united medially in *Acanthostichus* behind the distal margin. *Acanthostichus* has on each lobe of the labrum a rounded tubercle that extends over and beyond the distal margin (fig. 102). Such structures are lacking in the other species.

Mandible. The shape of the mandible is similar in all of the species examined except *Cylindromyrmex* (fig. 112). Each mandible has a distinct basal and masticatory margin, which is irregular in such a way that teeth are poorly defined. The setae are never great in number, and the trulleum and mandalus are present in all cases.

Maxilla. The maxillary palpus is 2-segmented in each species except *Sphinctomyrmex steinheili* (fig. 117) where it is 3-segmented. The shape of segment II of the 2-segmented palpi is similar in all 4 species (figs. 99, 106, 109, 114). The shape of the stipes is similar in all 5 species and each possesses a transverse groove (figs. 99, 106, 109, 114). A number of setae are inserted along the lateral margin in each of the species except *Cerapachys opaca*. The stipes is heavily sclerotized. The galea varies little in shape between the species, and the galeal crown is flattened and bears numerous setae. The galeal comb is most prominent in *Acanthostichus* sp. (fig. 101) and consists of more than 15 uniquely shaped setae. While the galeal comb is less prominent in *Cerapachys* (figs. 106, 110), it is almost absent in *Sphinctomyrmex* (fig. 117). The lacinia is triangular, and the lacinial comb varies primarily in the forms of setae that compose it. The lacinial gonia in each species bears 1 or more setae.

Labium. The labial palpus is 2-segmented in *Cerapachys* (figs. 103, 111) and 3-segmented in *Acanthostichus* (fig. 100), *Cylindromyrmex* (fig. 113), and *Sphinctomyrmex* (fig. 119). The premental shield is weakly sclerotized and bears several long setae. The proximal lateral angles of the shield are elongated, and articulate with the poorly defined epimental sclerites. Raquettes are not present. Subglossal brushes are present and consist of numerous large setae. Paraglossae and paraglossal pegs are absent in the species examined.

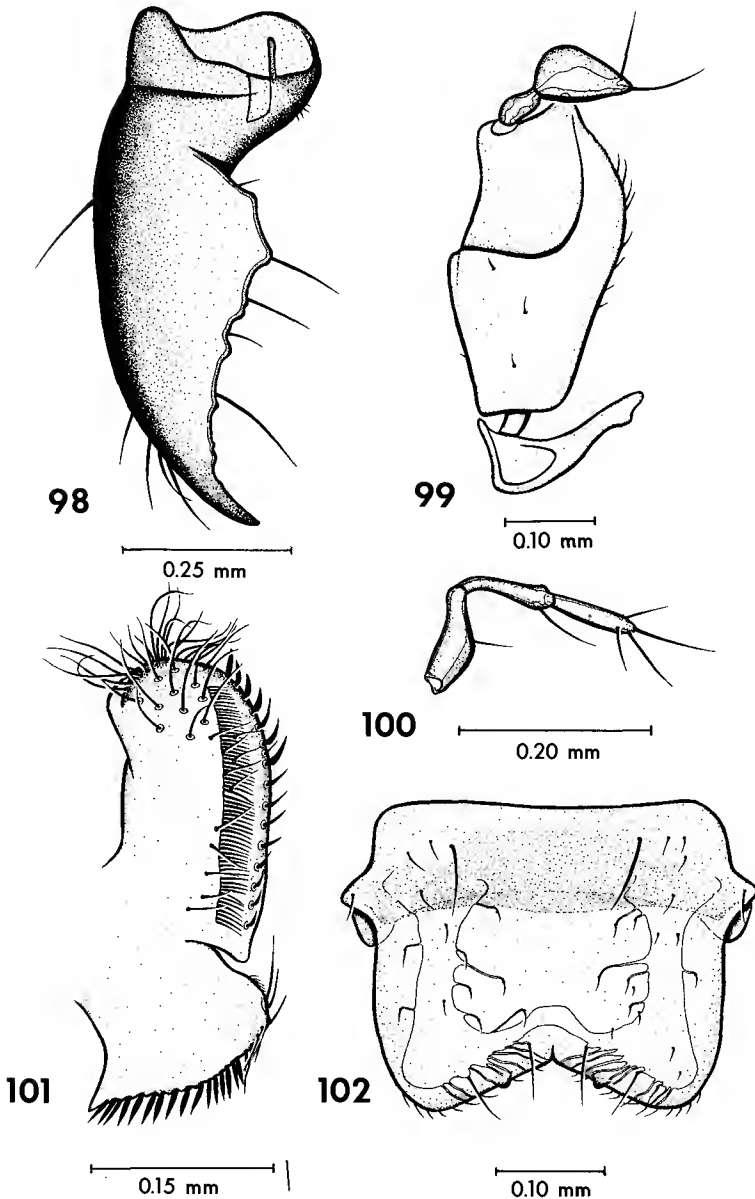


Plate 28. *Acanthostichus* sp. near *quadratus* (worker).

- Fig. 98. Right mandible, dorsal view.
 Fig. 99. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 100. Right labial palpus, lateral view.
 Fig. 101. Left galea and lacinia, external view.
 Fig. 102. Labrum, external view.

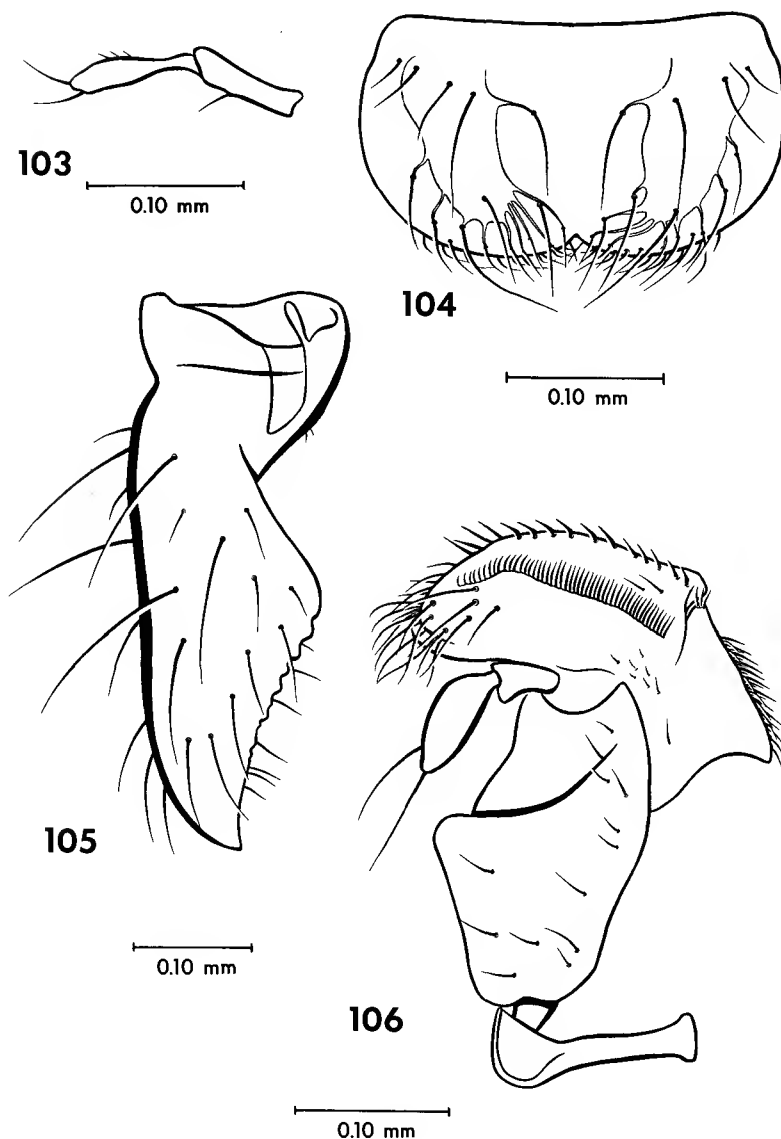


Plate 29. *Cerapachys opaca* (worker).

Fig. 103. Left labial palpus, lateral view.

Fig. 104. Labrum, external view.

Fig. 105. Right mandible, dorsal view.

Fig. 106. Left maxilla, external view.

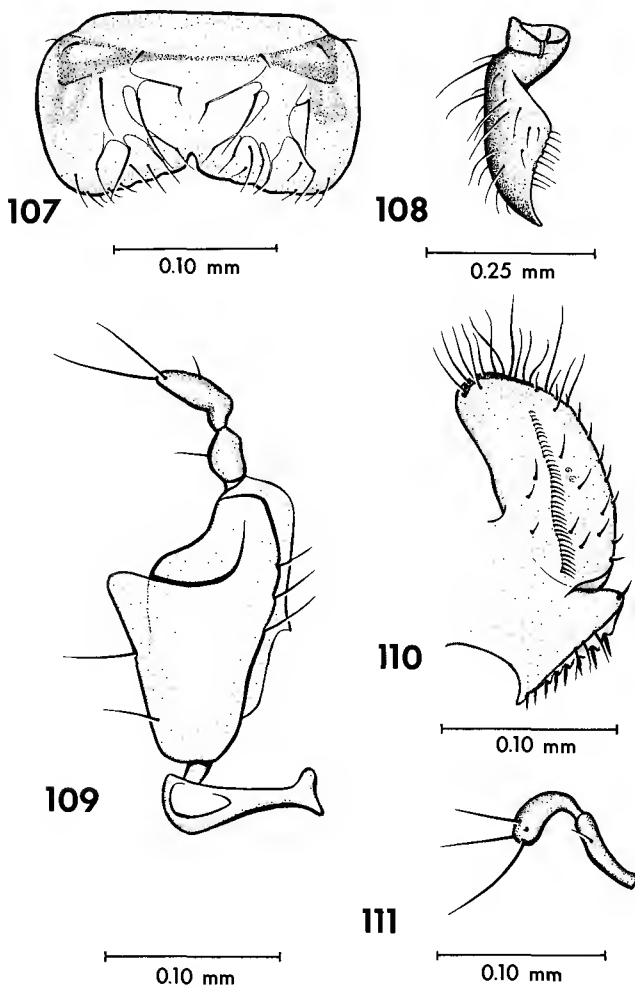


Plate 30. *Cerapachys* n.sp. (worker).

- Fig. 107. Labrum, external view.
 Fig. 108. Right mandible, dorsal view.
 Fig. 109. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 110. Left galea and lacinia, external view.
 Fig. 111. Left labial palpus, lateral view.

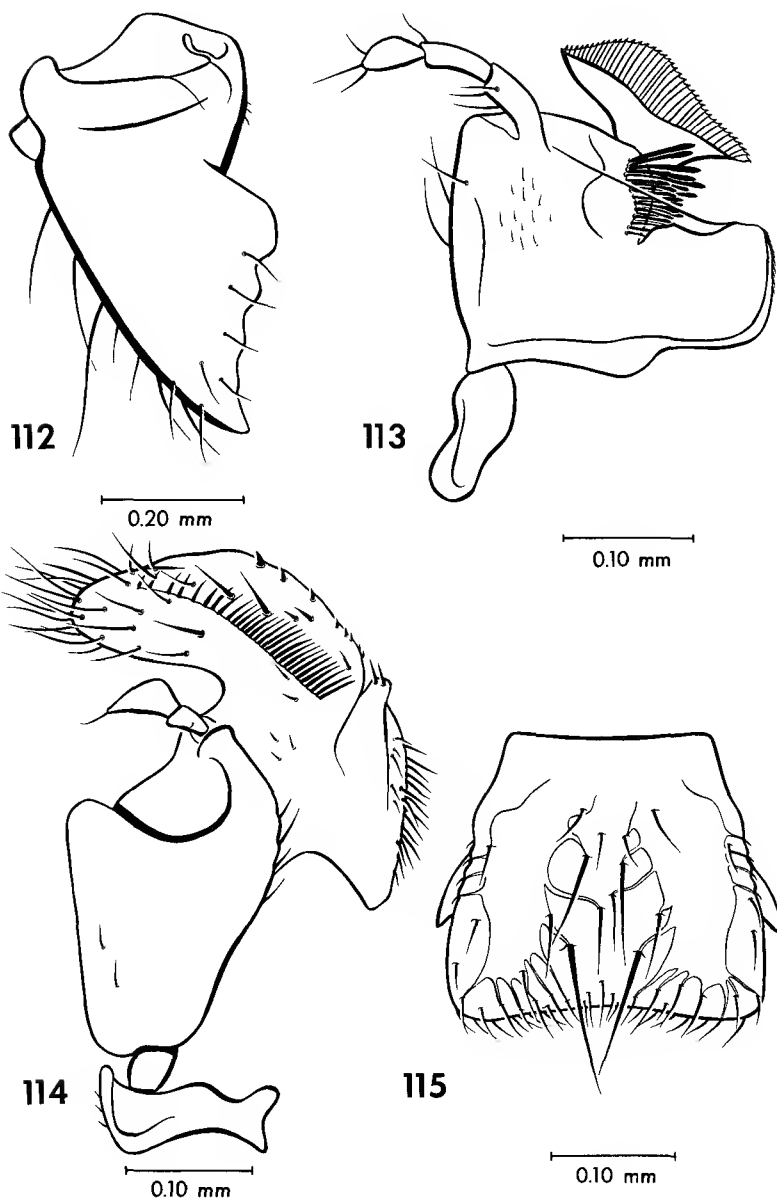


Plate 31. *Cylindromyrmex striatus* (worker).

Fig. 112. Right mandible, dorsal view.

Fig. 113. Labium with left labial palpus, lateral view.

Fig. 114. Left maxilla, external view.

Fig. 115. Labrum, external view.

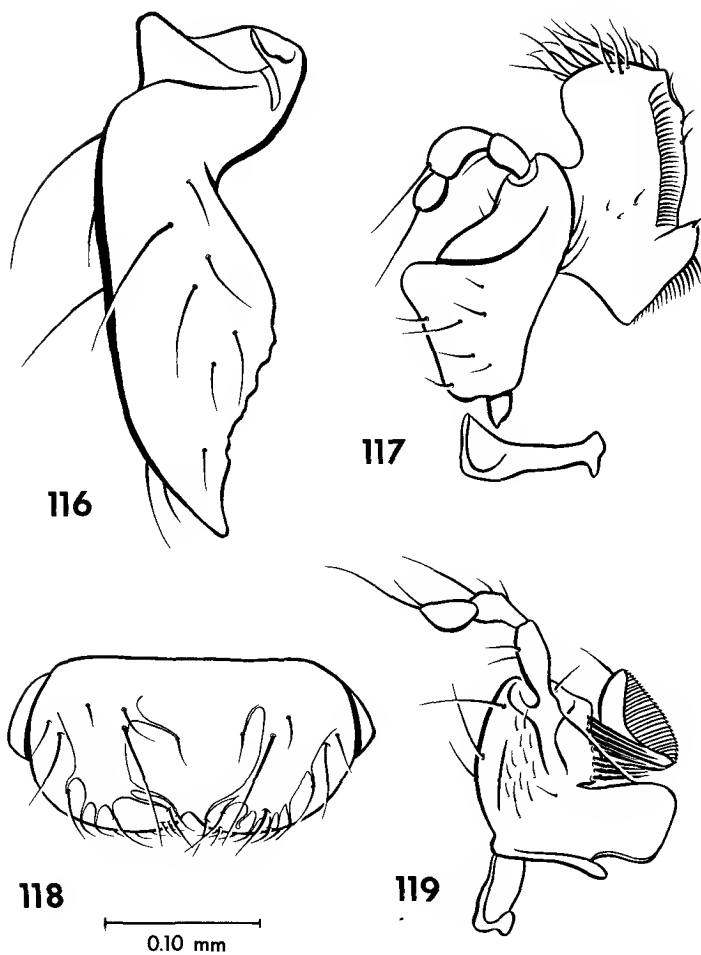


Plate 32. *Sphinctomyrmex steinheili* (worker).

- Fig. 116. Right mandible, dorsal view.
Fig. 117. Left maxilla, external view.
Fig. 118. Labrum, external view.
Fig. 119. Labium with left labial palpus, lateral view.

Subfamily Dorylinae

Tribe Aenictini

Species examined:

<i>Aenictus alticolus</i> (worker)	<i>A. laeviceps</i> (worker)
<i>A. aratus</i> (worker) (Plate 33)	<i>A. philippinensis</i> (worker)
<i>A. ceylonicus</i> (worker)	<i>A. rotundatus</i> (worker) (Plate 35)
<i>A. dentatus</i> (worker)	<i>A. wroughtoni</i> (worker)
<i>A. gracilis</i> (worker, queen) (queen, Plate 34)	<i>A. sp.</i> (male) (Plate 36)

Labrum. The labrum has 2 forms in *Aenictus*. One is emarginate and medially cleft on the distal margin (fig. 120), the cleft being narrow and slitlike. The second type is smoothly emarginate without a cleft (fig. 130). Species that have the cleft labrum are *A. aratus* (fig. 120), *A. dentatus*, *A. gracilis* (both worker and queen) (fig. 129), and *A. philippinensis*. The hemocoel consists of 2 arms, one extending into each lobe, that are united across the middle of the labrum in *A. aratus*. The labrum is without tubercles.

Mandible. Three types of mandibles are found in *Aenictus*. One is narrow with 3 or 4 teeth as in *A. ceylonicus*. The remaining 2 types are broader and triangular; in one of these the basal and masticatory angles meet almost at a right angle [*A. aratus* (fig. 122), *A. dentatus*, *A. philippinensis*, and *A. rotundatus* (fig. 132)], and in the other, the basal margin curves smoothly into the masticatory margin (*A. alticolus*, *A. gracilis*, *A. laeviceps*, and *A. wroughtoni*). In both of these 2 types, the masticatory margins are usually provided with an apical tooth and numerous subapical teeth. The mandibles of the queen and the male differ widely from those of the workers. In the sexes, the mandible is elongated and pointed apically without distinct basal and masticatory margins (figs. 126, 136). The male mandible is broad, with abundant, long setae. The trulleum and mandalus are present in all species and castes examined.

Maxilla. The palpus is 2-segmented in all castes of all species examined, including the queen and the male. Palpal segment I is short and cylindrical, while segment II in the workers and the queen is longer and rodlike (figs. 124, 127, 134). In the male this second segment is proportionately shorter (fig. 140). The stipes is most commonly shaped as it is in *A. aratus* (fig. 124). The lateral shoulder is usually distinct, and even when less conspicu-

ously formed, it always bears 1 or more stout setae. This is true also for the queen and the male. The proximal half of the external surface usually bears 1 or more long setae; in the male these may number 7 or more. No transverse groove is present on the stipites in *Aenictus*. The galea is of relatively constant shape throughout the genus. The galeal crown is usually less flattened in *Aenictus* than it is in the Ponerinae, and bears numerous long setae. Each species examined, with the exception of *A. rotundatus*, possesses what might be considered a galeal comb. Although this may comprise only 1 or 2 setae, it is identified as a comb because of the distinctive shape and size of the setae. Both the queen and the male have the comb, and it may also be present in some workers of *A. rotundatus*; it was absent in the specimen examined. The lacinia can be subtriangular and rounded posteriorly as in *A. rotundatus* (fig. 131), or it can be triangular as in *A. dentatus* and *A. philippinensis*. The lacinial comb is usually irregular, although in *A. aratus* there is a regular row of heavy setae in addition to the thinner, irregularly placed setae (fig. 121). This comb was absent in the male examined. The lacinial gonia may or may not bear 1 or more short setae.

Labium. The labial palpus is 2-segmented in the workers (figs. 123, 125, 133, 135), although in *A. laeviceps* the segments appear partially fused. In the queen and male, the palpus is 1-segmented (figs. 128, 138). In all species examined, including the queen and male, segment II bears a conspicuous sensory peg. This peg is located on or near the apex of the segment, except in *A. alticolus* and *A. laeviceps* where it is located at about the middle of the segment. The shape of the 2-segmented palpus is constant throughout the species examined. The premental shield is lightly sclerotized and is shaped as in *A. rotundatus* (fig. 135). The epimental sclerites are present, although not always distinct, and the raquettes are absent. Subglossal brushes are always present but do not consist of large numbers of setae (fig. 125). Paraglossae and/or paraglossal sensory pegs are absent.

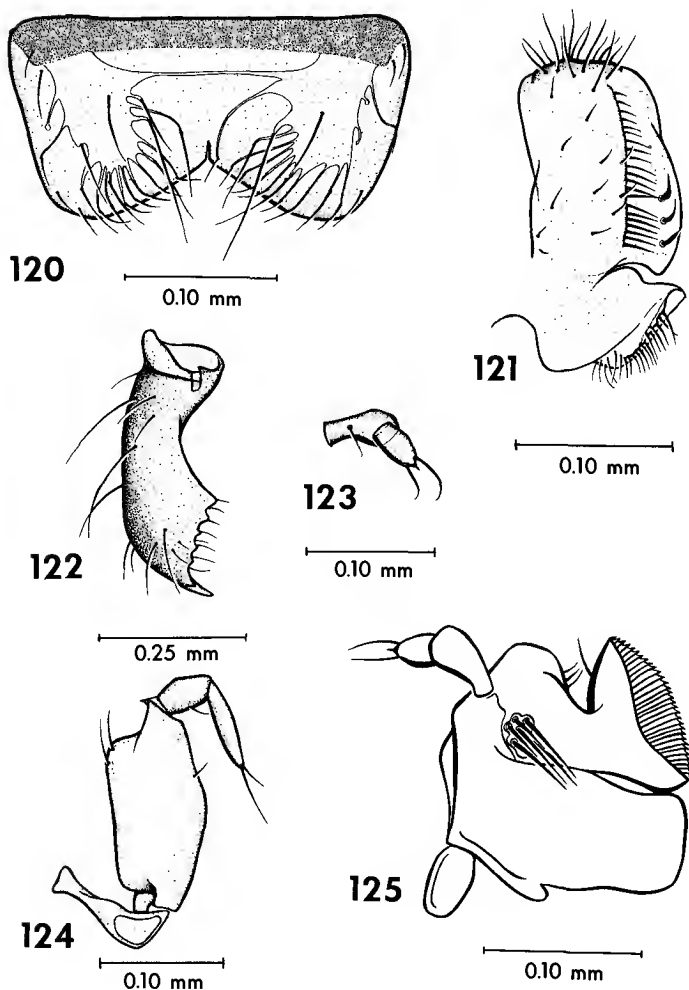


Plate 33. *Aenictus aratus* (worker).

- Fig. 120. Labrum, external view.
 Fig. 121. Left galea and lacinia, external view.
 Fig. 122. Right mandible, dorsal view.
 Fig. 123. Left labial palpus, lateral view.
 Fig. 124. Right stipes, maxillary palpus, and cardo, external view.
 Fig. 125. Labium with left labial palpus, lateral view.

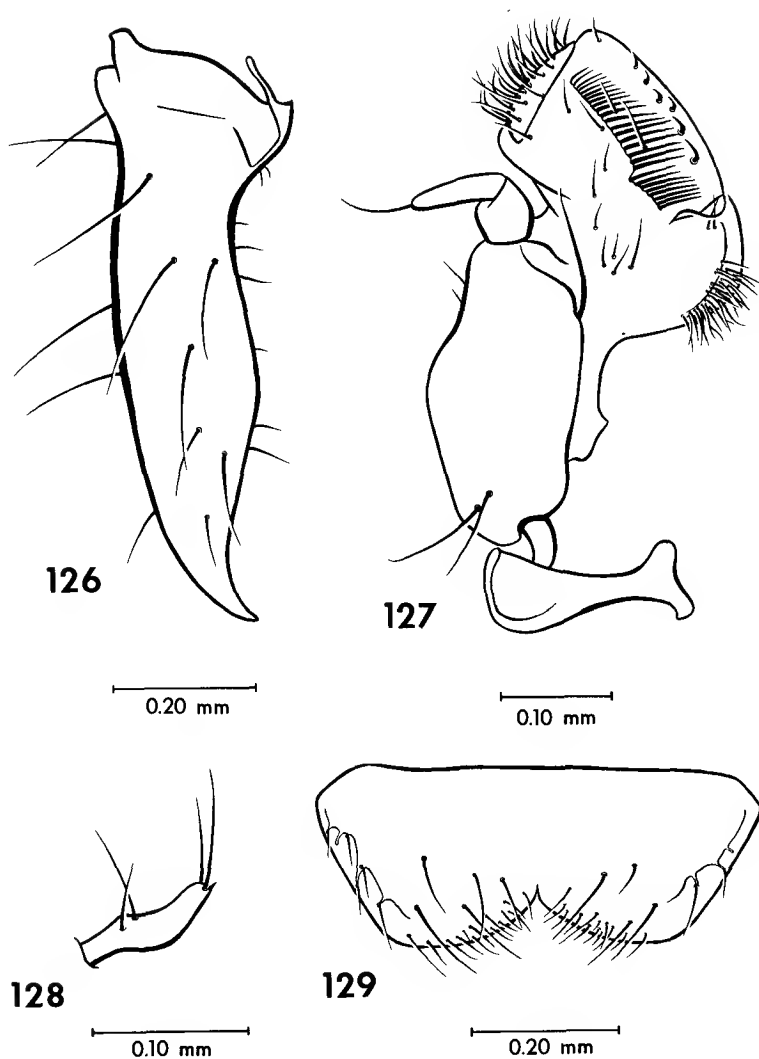


Plate 34. *Aenictus gracilis* (queen).

- Fig. 126. Right mandible, dorsal view.
Fig. 127. Left maxilla, external view.
Fig. 128. Left labial palpus, ventral view.
Fig. 129. Labrum, external view.

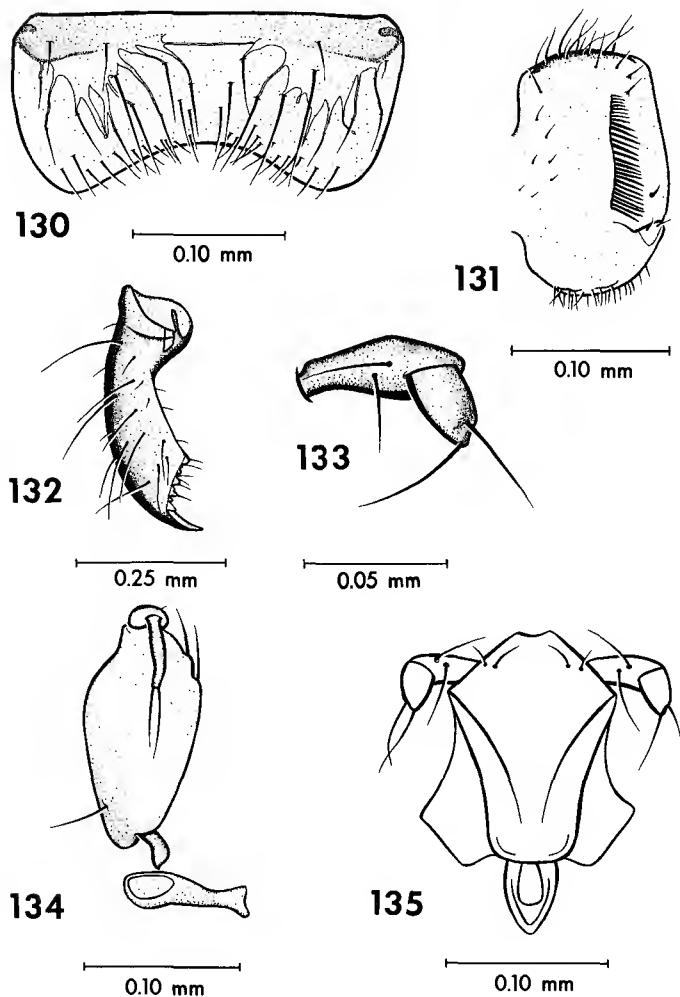


Plate 35. *Aenictus rotundatus* (worker).

- Fig. 130. Labrum, external view.
 Fig. 131. Left galea and lacinia, external view.
 Fig. 132. Right mandible, dorsal view.
 Fig. 133. Left labial palpus, ventral view.
 Fig. 134. Left stipes, maxillary palpus and cardo, external view.
 Fig. 135. Labium, ventral view.

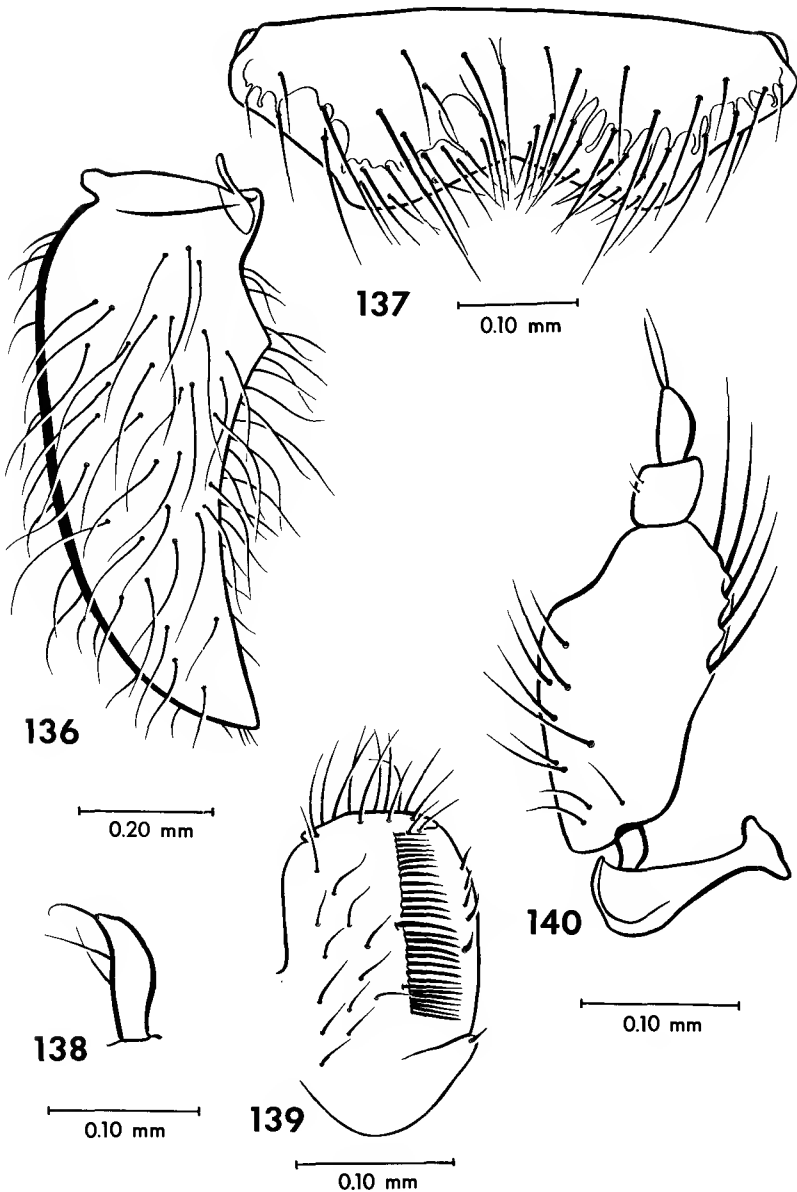


Plate 36. *Aenictus* sp. (male).

- Fig. 136. Right mandible, dorsal view.
 Fig. 137. Labrum, external view.
 Fig. 138. Left labial palpus, lateral view.
 Fig. 139. Left galea and lacinia, external view.
 Fig. 140. Left stipes, maxillary palpus, and cardo, external view.

Tribe Dorylini

Species examined:

- Aenictogiton* sp. (male) (Plate 37)
Dorylus (*Alaopone*) *orientalis* (worker) (Plate 38)
Dorylus (*Anomma*) *emeryi* (soldier)
Dorylus (*Anomma*) *wilverthi* (soldier) (Plate 39)
Dorylus (*Dichthadia*) *laevigatus* (worker) (Plate 40)
Dorylus (*Dorylus*) *brevipennis* (queen) (Plate 41)
Dorylus (*Dorylus*) *helvolus* (soldier, worker) (soldier, Plate 42)
Dorylus (*Typhlopone*) *fulvus* (male) (Plates 43, 44)
Dorylus (*Typhlopone*) *labiatus* (soldier, queen) (queen, Plate 45)
Dorylus (*Typhlopone*) *dentifrons* (soldier, worker) (Plates 46, 47)

Labrum: The distal margin is smoothly curved, not emarginate, and is without a median cleft. Labral tubercles are present in all workers and soldiers, but absent in males and queens. In the subgenus *Anomma*, the soldiers have a single, median tubercle near the distal margin (fig. 150). This is also true for workers and soldiers of *D. (Dorylus) helvolus* (fig. 165). While the worker of *D. (Alaopone) orientalis* (fig. 146) has a single median projection, this structure is clearly a lamina-like extension of the cuticle. The nature of the other tubercles is not clear. In *D. (Typhlopone) dentifrons* workers and the soldiers, there are 3 tubercles (figs. 180, 185), and in *D. (Dichthadia) laevigatus*, there are 2 (fig. 155). But the median structure seems to be similar to that of *D. (Alaopone) orientalis*, and thus different from the lateral tubercles. In the *D. (Typhlopone) labiatus* soldier, the tubercles are reduced, and the labrum of the queen of *D. (Typhlopone) labiatus* (fig. 174) is distinctive in having 2 large lamina-like projections. The labrum of the male of *D. (Typhlopone) fulvus* is extraordinarily thick at its distal margin (fig. 169). The hemocoel consists of 2 arms that unite medially, close to the distal margin.

Mandible. There is no distinct basal margin. The masticatory margin is commonly irregular, as in the soldier of *D. (Dorylus) helvolus* (fig. 164), and usually bears an apical tooth and 1 conspicuous subapical tooth. The soldiers of *Anomma* have falcate mandibles with both an apical tooth and a subapical tooth (fig. 152). Male mandibles are broad proximally, as in *Aenictogiton* (fig. 141) and *D. (Typhlopone) fulvus* (fig. 170), and are pointed at the apex. The queen mandibles are similar (figs. 160, 175). The trulleum and mandalus are always present.

Maxilla. The maxillary palpus is 2-segmented in all species and castes examined except *Aenictogiton* sp. (male) (fig. 144) and *D. (Alaopone) orientalis* (worker) (fig. 149), where it is 1-segmented. In the male of *D.*

(*Typhlopone*) *fulvus* (fig. 171), these 2 segments apparently have undergone considerable fusion. In *Dorylus* the palpus is typically short, as in *D. (Typhlopone) dentifrons* (figs. 179, 184). In all species examined there is a prominent transverse stipital groove (e.g., fig. 153). The lateral shoulder of the stipes always bears several stout setae. One or more stout setae are also common on the proximal external face. The stipites are heavily sclerotized. The galea is usually shaped as in *D. (Typhlopone) dentifrons* (figs. 183, 188), and the galeal crown is prominent, swollen, and often covered by setae-bearing verrucae. The galeal crown is most highly modified in the soldiers of *D. (Anomma) emeryi* and *wilverthi* (fig. 154), *D. (Typhlopone) labiatus* and *dentifrons* (figs. 183, 188), and in the workers of *D. (Dichthadia) laevigatus* (fig. 157), where it is produced into a conical prominence. The lacinia of *D. (Dorylus) helvulus* (fig. 168) is typical of soldiers and workers. The lacinial comb is conspicuous, with many stout setae. In the queens examined, the lacinia is of modified shape and the comb has fewer setae (figs. 162, 178). The male of *D. (Typhlopone) fulvus* (fig. 172) possesses a lacinia whose comb is reduced to 1 stout seta and 1 small, hooklike seta, while in the *Aenictogiton* male (fig. 145) the lacinial comb is prominent. The lacinial gonion may or may not be provided with 1 or more short setae.

Labium. The labial palpus is 2-segmented in all workers and soldiers and 1-segmented in queens and males. The segments of the 2-segmented palpi are long and rodlike (e.g., fig. 151), while the 1-segmented palpus is narrowed proximally and expanded distally (e.g., fig. 161). The premental shield is moderately sclerotized, and the epimental sclerites are distinct in part. Raquettes are absent as are paragossae and/or paraglossal sensory pegs. Prominent subglossal brushes are always present.

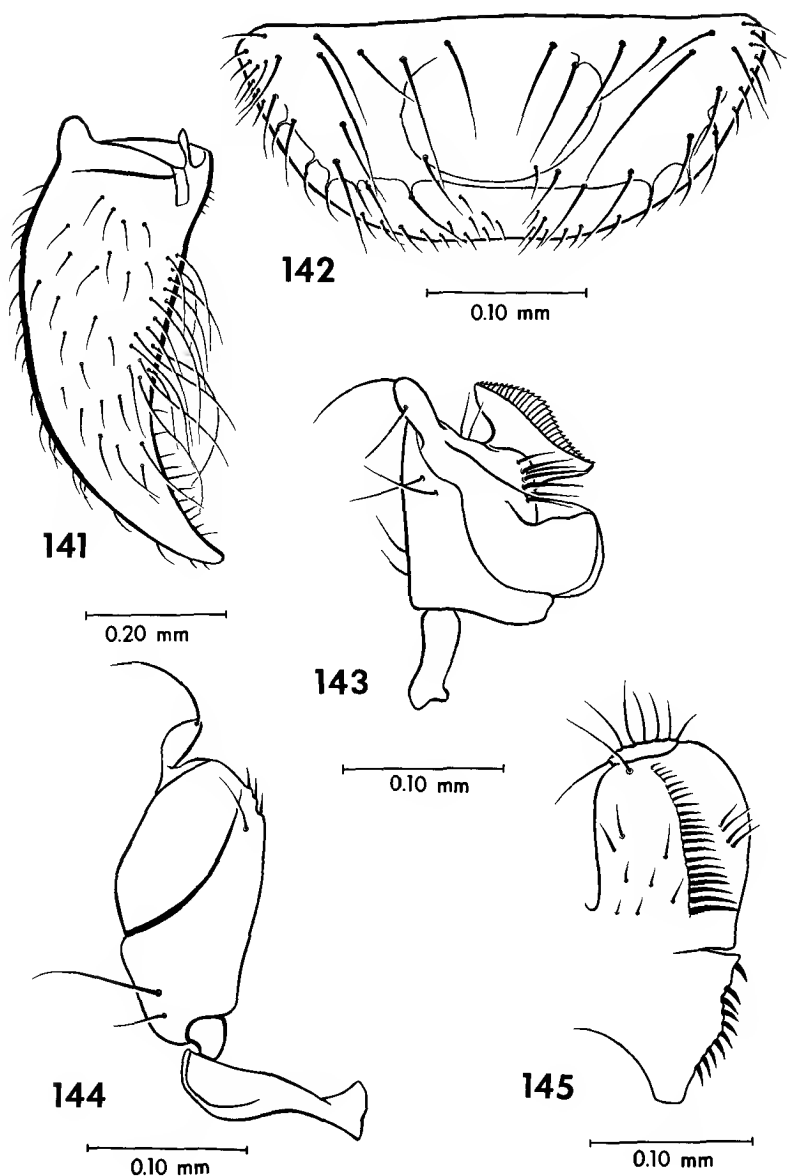


Plate 37. *Aenictogiton* sp. (male).

- Fig. 141. Right mandible, dorsal view.
 Fig. 142. Labrum, external view.
 Fig. 143. Labium with left labial palpus, lateral view.
 Fig. 144. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 145. Left galea and lacinia, external view.

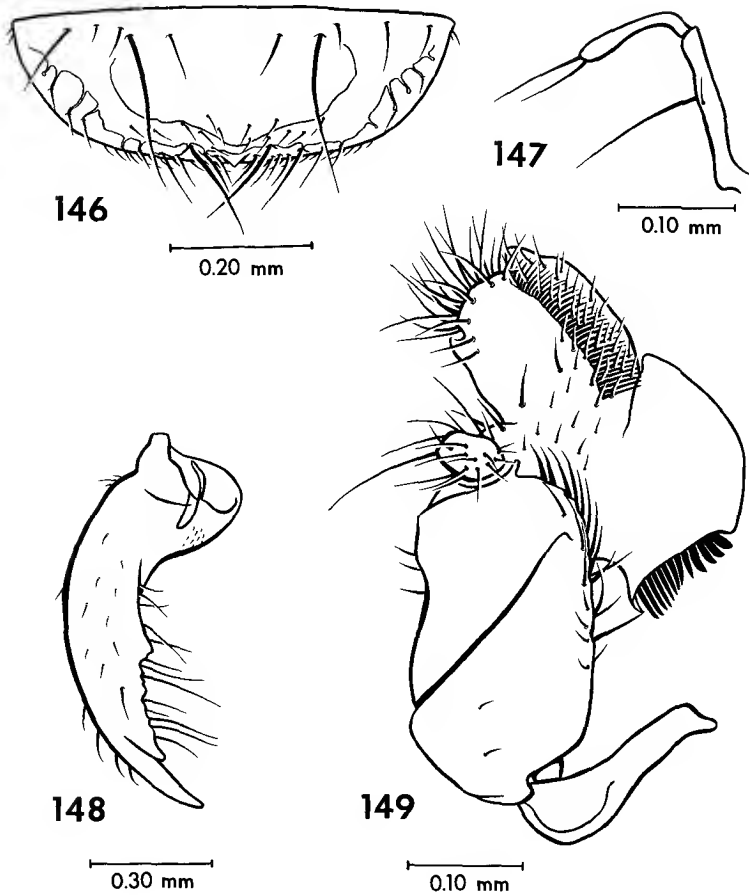


Plate 38. *Dorylus (Alaopone) orientalis* (worker).

- Fig. 146. Labrum, external view.
Fig. 147. Left labial palpus, lateral view.
Fig. 148. Right mandible, dorsal view.
Fig. 149. Left maxilla, external view.

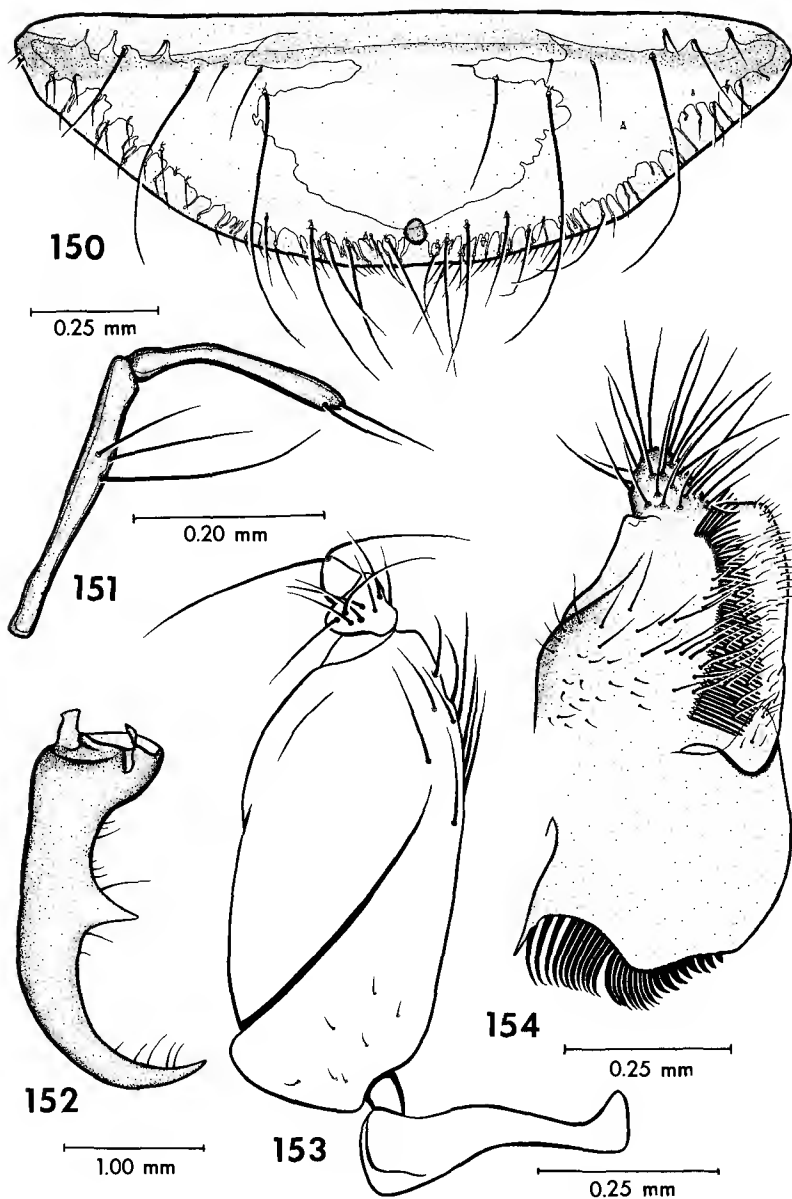


Plate 39. *Dorylus (Anomma) wilverthi* (soldier).

- Fig. 150. Labrum, external view.
 Fig. 151. Right labial palpus, lateral view.
 Fig. 152. Right mandible, dorsal view.
 Fig. 153. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 154. Left galea and lacinia, external view.

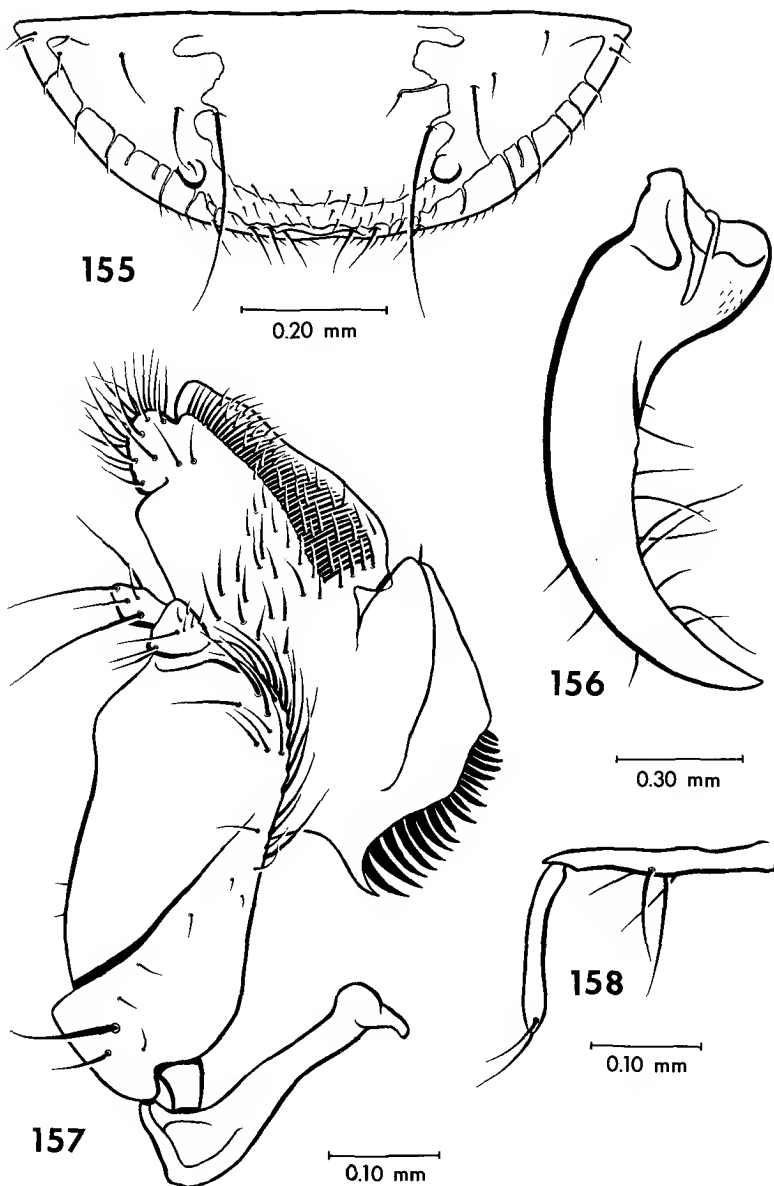


Plate 40. *Dorylus (Dichthadia) laevigatus* (worker).

- Fig. 155. Labrum, external view.
Fig. 156. Right mandible, dorsal view.
Fig. 157. Left maxilla, external view.
Fig. 158. Left labial palpus, lateral view.

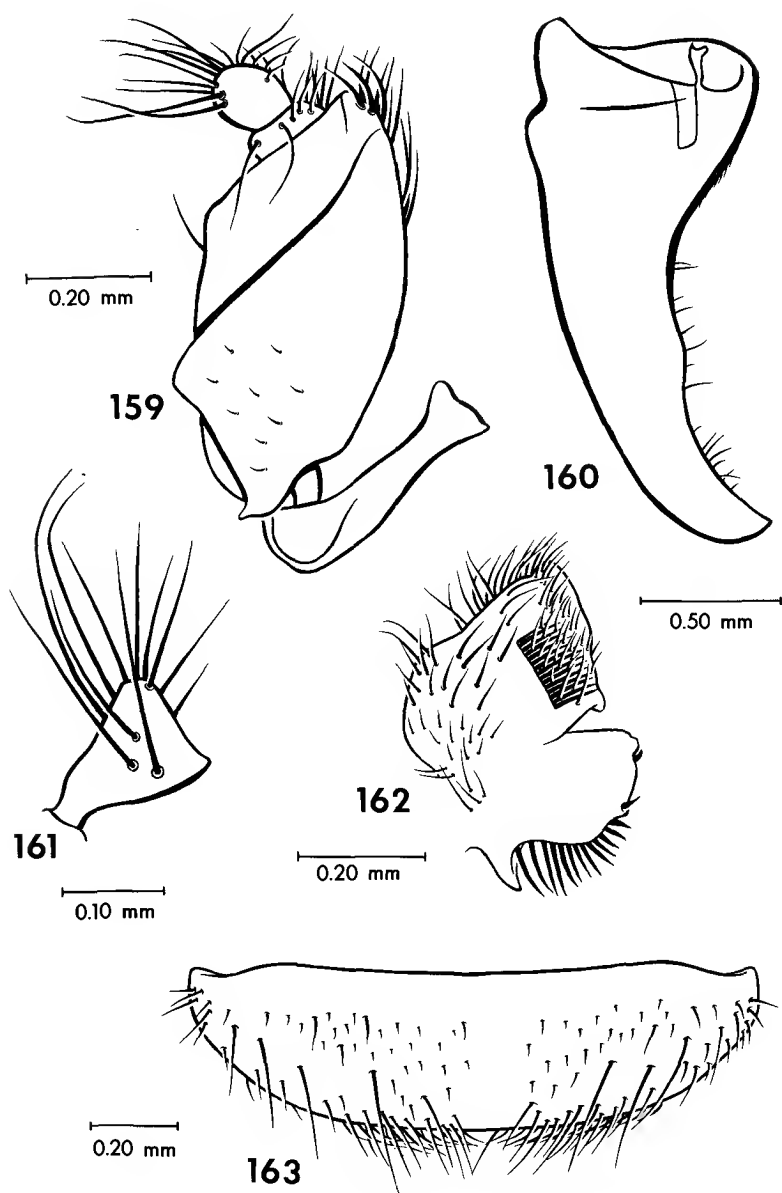


Plate 41. *Dorylus (Dorylus) brevipennis* (queen).

- Fig. 159. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 160. Right mandible, dorsal view.
 Fig. 161. Left labial palpus, ventral view.
 Fig. 162. Left galea and lacinia, external view.
 Fig. 163. Labrum, external view.

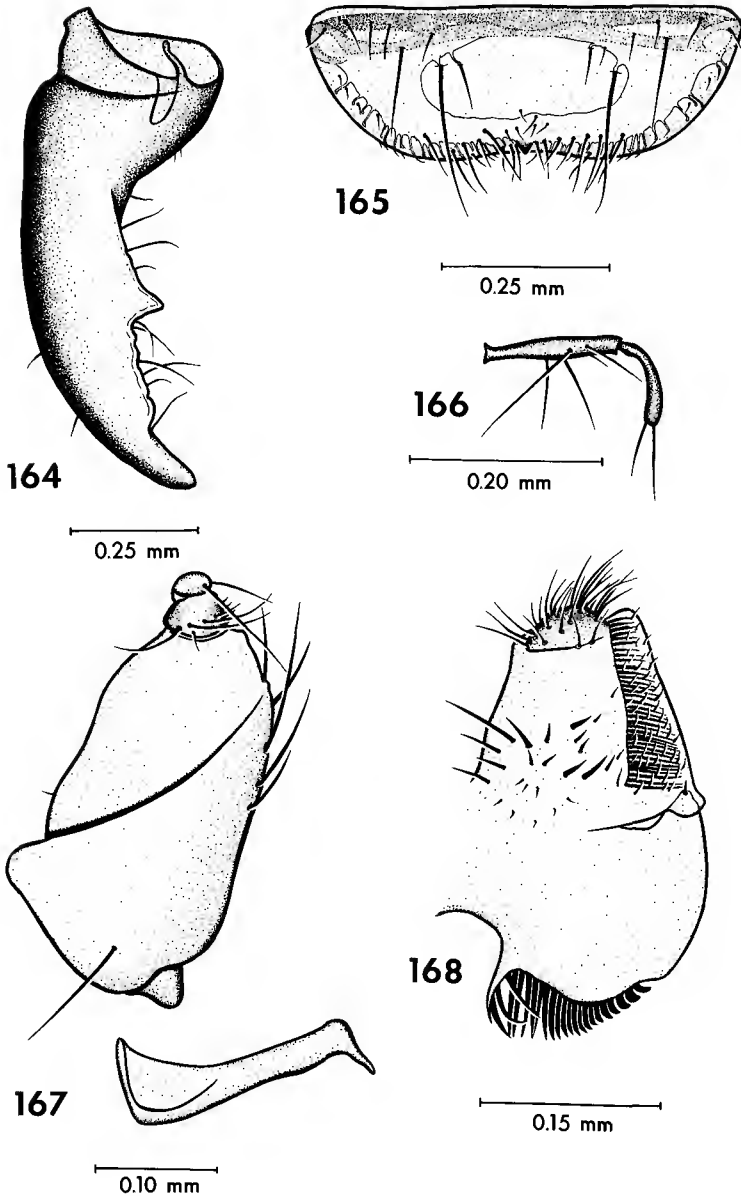


Plate 42. *Dorylus (Dorylus) helvolus* (soldier).

Fig. 164. Right mandible, dorsal view.

Fig. 165. Labrum, external view.

Fig. 166. Right labial palpus, lateral view.

Fig. 167. Left stipes, maxillary palpus, and cardo, external view.

Fig. 168. Left galea and lacinia, external view.

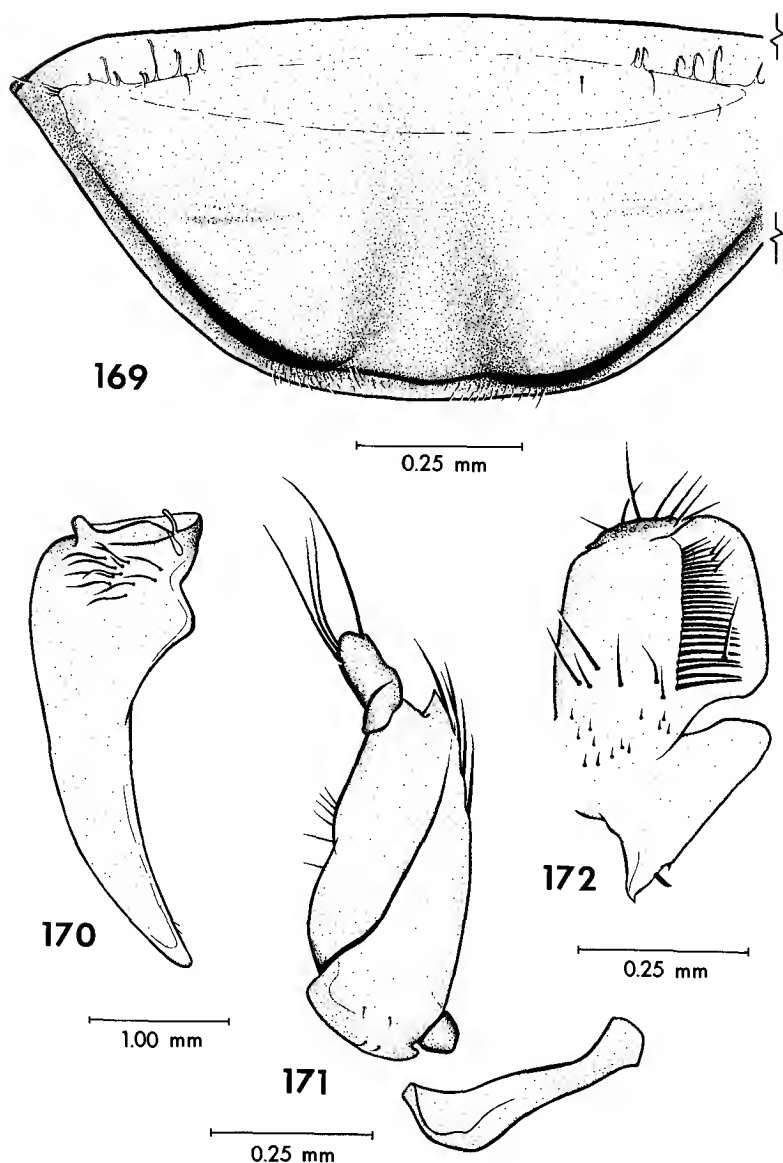


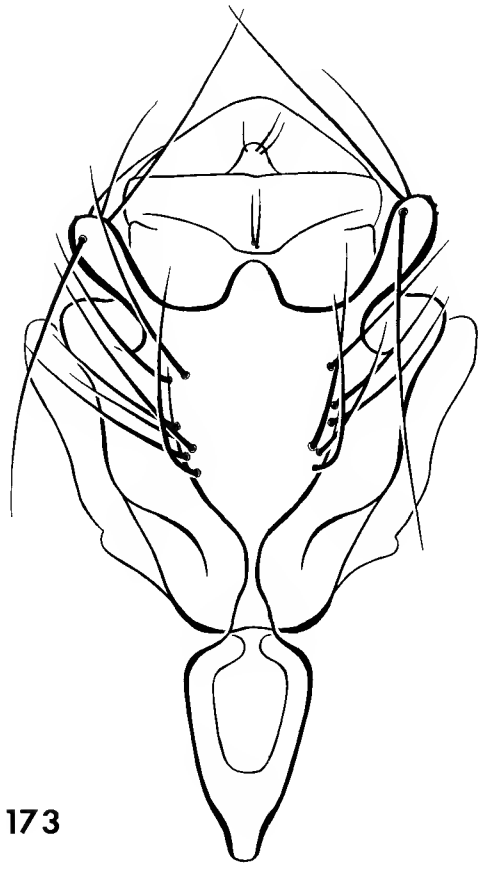
Plate 43. *Dorylus (Typhlopone) fulvus* (male).

Fig. 169. Labrum, external view.

Fig. 170. Right mandible, dorsal view.

Fig. 171. Left stipes, maxillary palpus, and cardo, external view.

Fig. 172. Left galea and lacinia, external view.



173

0.10 mm

Plate 44. *Dorylus (Typhlopone) fulvus* (male).
Fig. 173. Labium, ventral view.

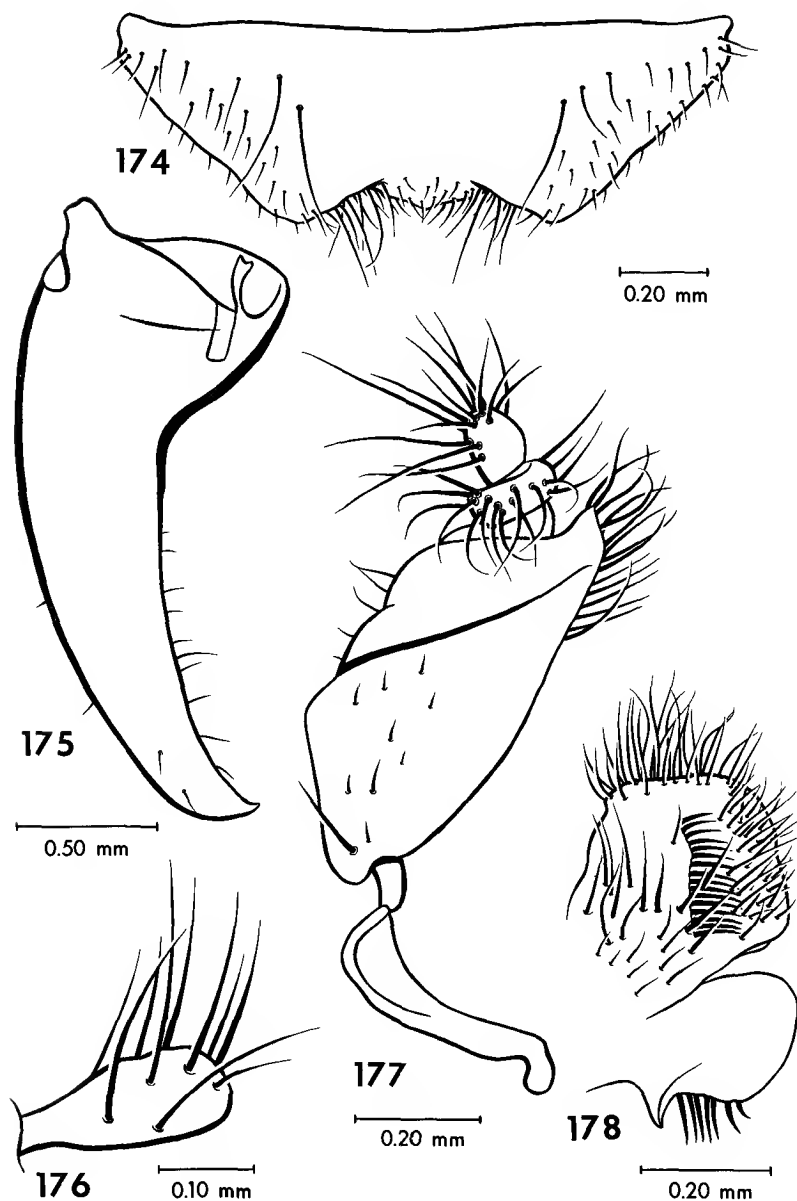


Plate 45. *Dorylus (Typhlopone) labiatus* (queen).

- Fig. 174. Labrum, external view.
 Fig. 175. Right mandible, dorsal view.
 Fig. 176. Left labial palpus, ventral view.
 Fig. 177. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 178. Left galea and lacinia, external view.

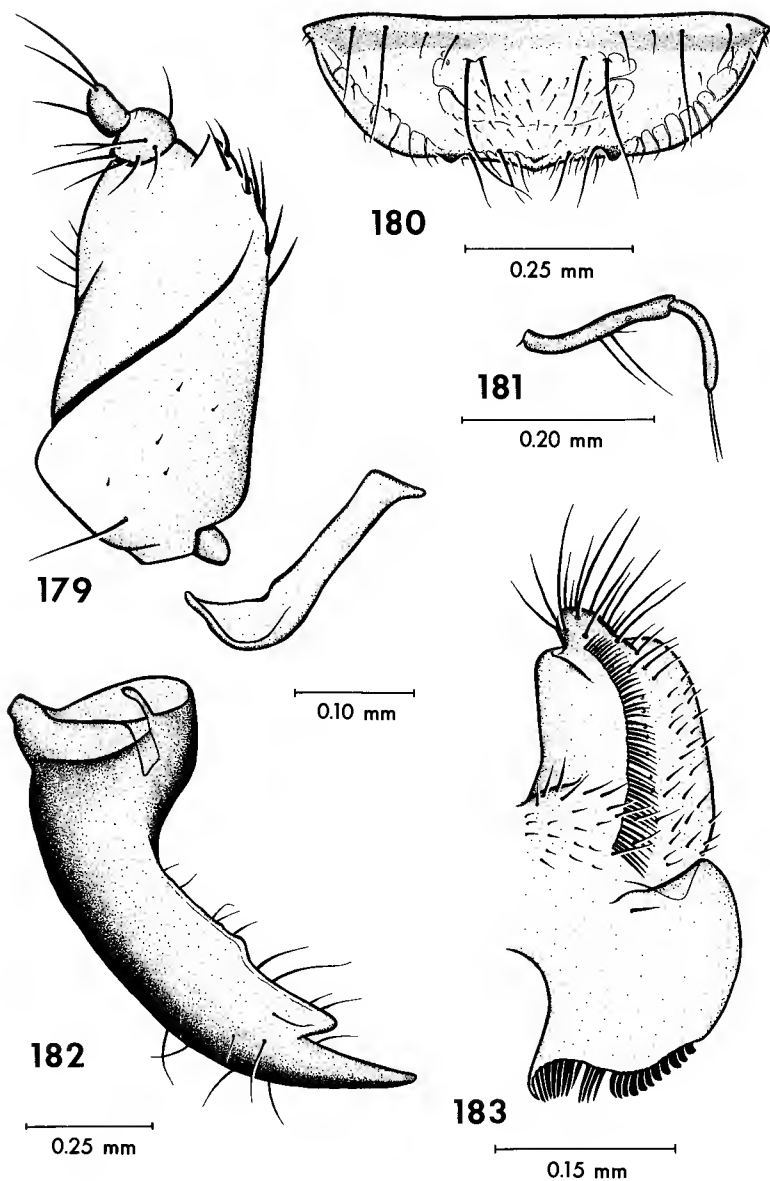


Plate 46. *Dorylus (Typhlopone) dentifrons* (soldier).

Fig. 179. Left stipes, maxillary palpus, and cardo, external view.

Fig. 180. Labrum, external view.

Fig. 181. Right labial palpus, lateral view.

Fig. 182. Right mandible, dorsal view.

Fig. 183. Left galea and lacinia, external view.

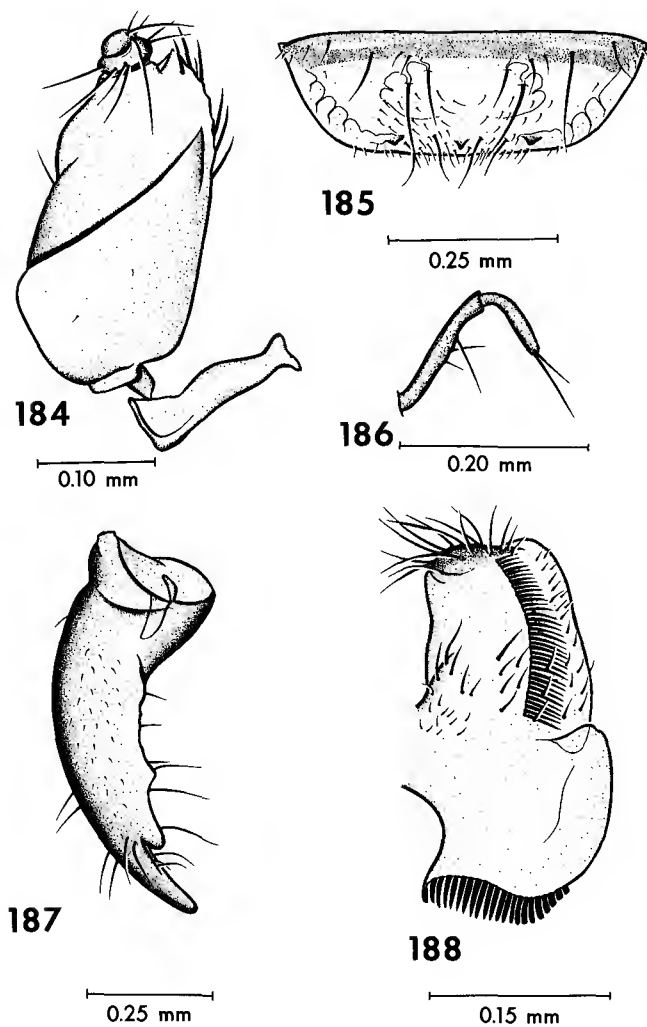


Plate 47. *Dorylus (Typhlopone) dentifrons* (worker).

- Fig. 184. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 185. Labrum, external view.
 Fig. 186. Right labial palpus, lateral view.
 Fig. 187. Right mandible, dorsal view.
 Fig. 188. Left galea and lacinia, external view.

Tribe Cheliomyrmecini – ns

Species examined:*Cheliomyrmex megalonyx* (soldier)*Cheliomyrmex morosus* (soldier, worker, male) (Plates 48–51)

Labrum. The labrum of soldiers and workers is emarginate and cleft (fig. 190), while that of the male is emarginate and cleftless (fig. 193). The labra of *C. megalonyx* and *C. morosus* are indistinguishable from one another. The shape of the male labrum is considerably different from that of the worker and soldier castes, and the hemocoel of the male occupies most of the labrum (fig. 193), whereas the hemocoel of the soldier and worker consists of 2 arms, one extending into each lobe and narrowly connecting behind the median cleft (fig. 190). Tubercles are present in the worker and soldier (fig. 190), but not in the male. Long setae are abundant on the external face of the male labrum.

Mandible. The mandible of the soldier is cylindrical and falcate with an apical tooth and 2 large subapicals (fig. 189). The mandibles of the soldiers of *C. megalonyx* and *C. morosus* are indistinguishable from one another. The worker mandible is flattened and triangular, with 1 apical and 2 subapical teeth. The masticatory margin is also provided with a series of denticles. The masticatory and basal margins are not clearly separated in either the worker or soldier. This is true also of the male, whose mandible is long, cylindrical, and falcate (fig. 194). With a single apical tooth, the internal margin of the mandible is smoothly curved proximad until it bulges out, forming a small shelf that bears a comb of rigid setae. The trulleum and mandalus are present in both species and in all castes examined, except in the male, which has no trulleum.

Maxilla. The maxillary palpus is 2-segmented in both species and all castes examined (figs. 191, 196). Although the shape of the stipes, in the soldiers and the workers examined, varies little, there is a detectable difference in the structure of the lateral shoulder between *C. megalonyx* and *C. morosus* (fig. 191). In each, the lateral shoulder bears 2 or 3 stout setae. A transverse groove on the surface divides the stipes into 2 parts. This stipital groove, however, is weakly developed in the soldiers and workers (fig. 191), and is totally absent in the male (fig. 196). The proximal external face of the stipes in the soldiers and workers bears 3 or 4 setae. The external surface of the male stipes bears numerous setae, and its lateral shoulder has 8 or more stout setae. The stipites are moderately sclerotized. The galea and lacinia are relatively constant in shape in both species and all castes (figs. 192, 195). The galeal crown is flattened and not prominent. It bears numerous setae. The galeal comb is present and conspicuous, and consists of 8 or more large and uniquely shaped setae (figs. 192, 195). The lacinial comb is composed of many small setae.

Labium. The labial palpus is 3-segmented in all cases (figs. 197, 198), although in the male of *C. morosus*, segments 2 and 3 are partially fused.

The premental shield is moderately sclerotized, and the epimental sclerites are generally well defined. In the male examined, there is a membranous expansion that might be called a raquette (fig. 198), but it does not seem to be an expansion of the distal end of the epimental sclerite. The subglossal brushes are prominent and are composed of large setae enlarged apically (figs. 197, 198). In the male, the ends of these setae may be truncated. Paraglossae and/or paraglossal pegs are absent.

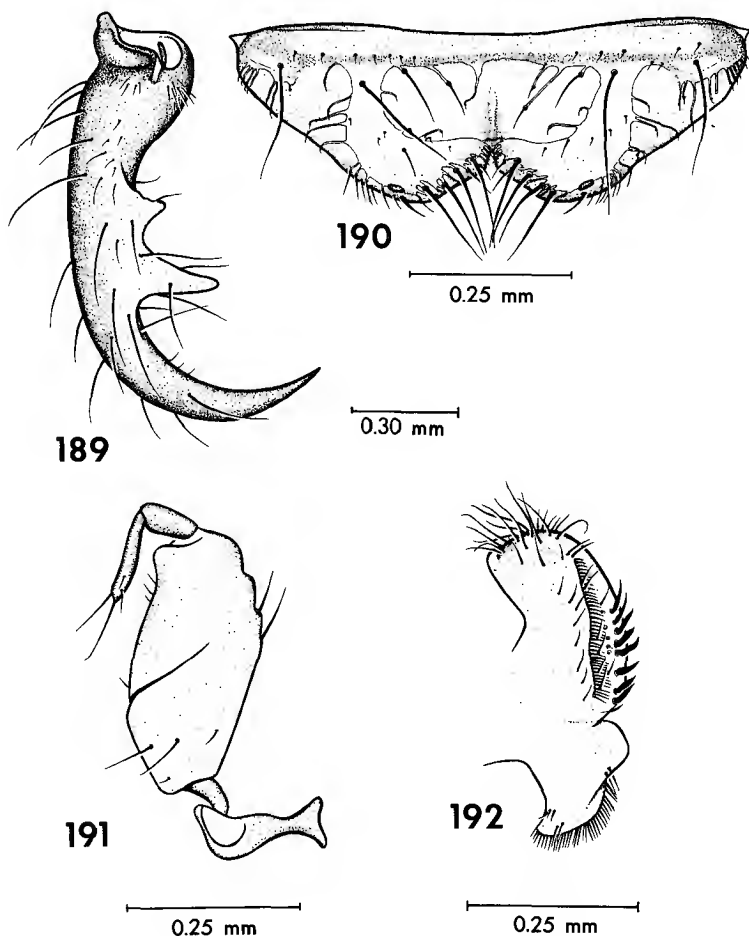


Plate 48. *Cheliomyrmex morosus* (soldier).

Fig. 189. Right mandible, dorsal view.

Fig. 190. Labrum, external view.

Fig. 191. Left stipes, maxillary palpus and cardo, external view.

Fig. 192. Left galea and lacinia, external view.

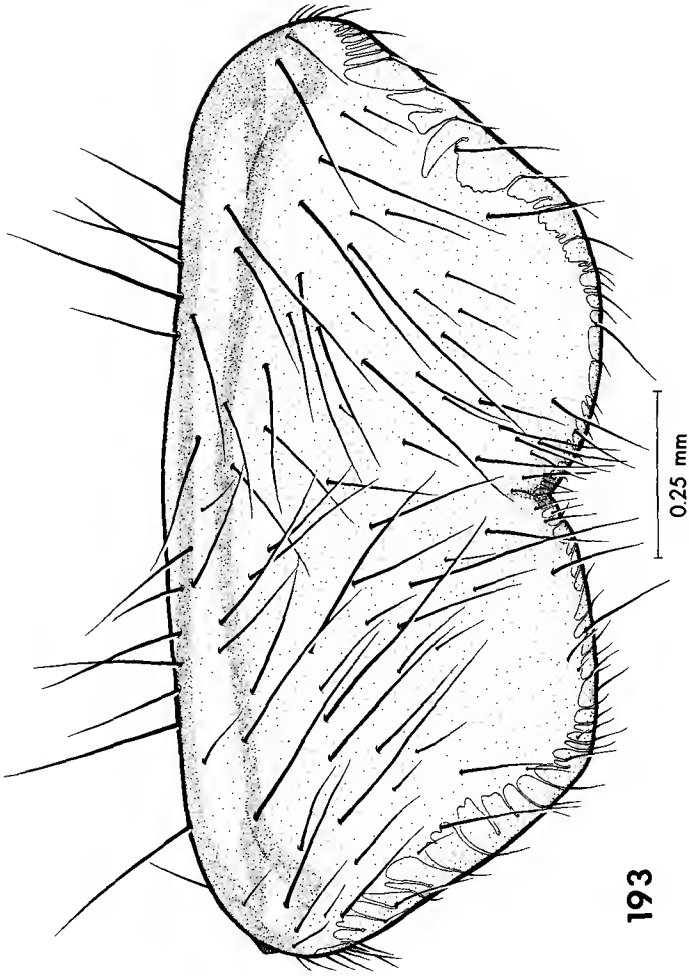


Plate 49. *Cheliomyrmex morosus* (male).

Fig. 193. Labrum, external view.

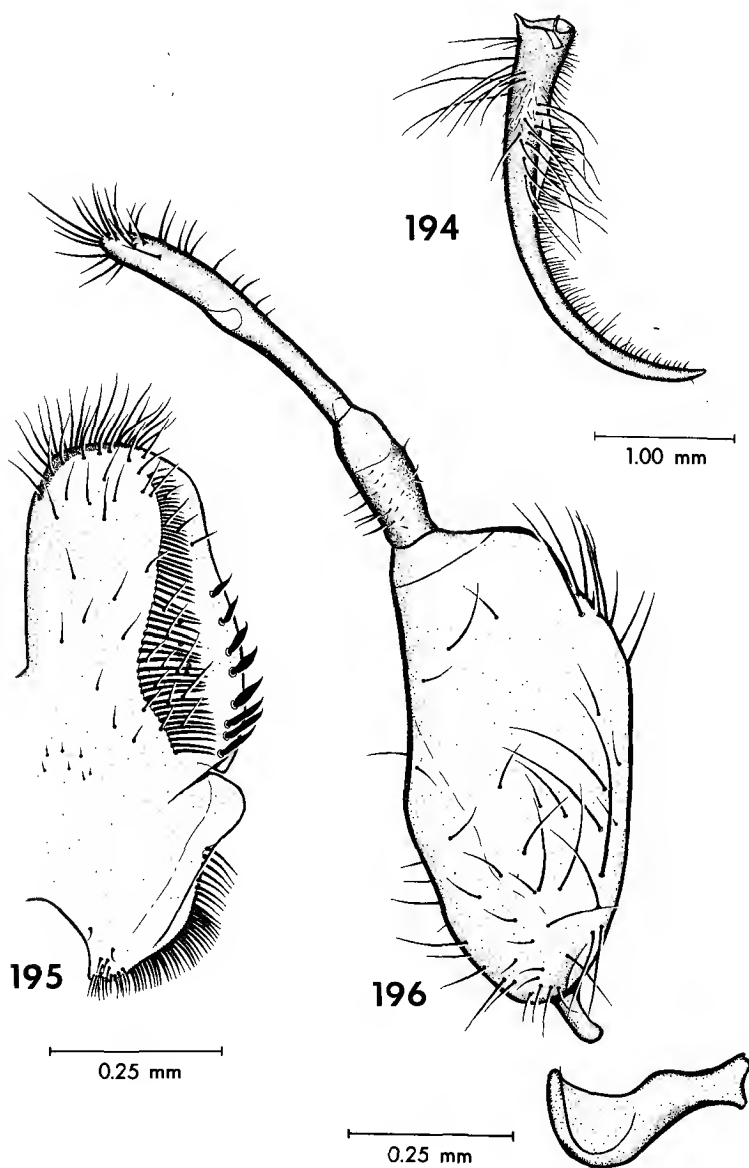


Plate 50. *Cheliomyrmex morosus* (male).

Fig. 194. Right mandible, dorsal view.

Fig. 195. Left galea and lacinia, external view.

Fig. 196. Left stipes, maxillary palpus, and cardo, external view.

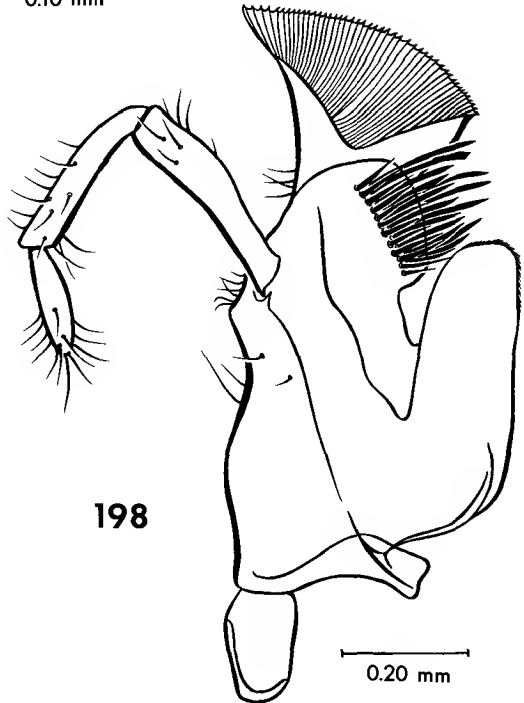
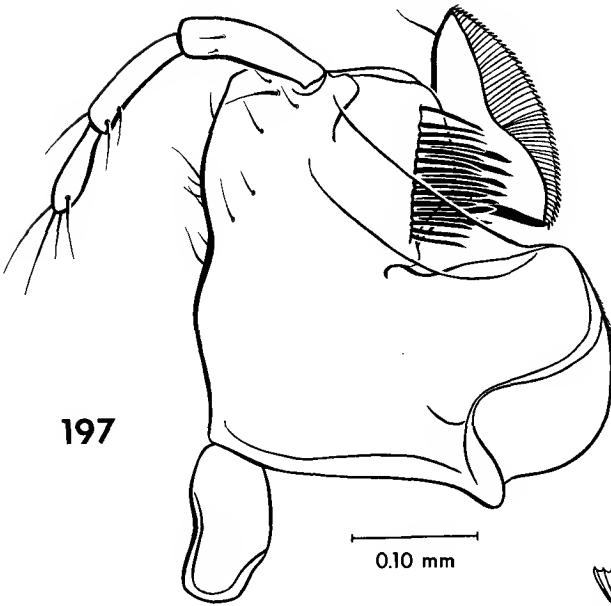


Plate 51. *Cheliomyrmex morosus*.

- Fig. 197. Soldier labium with left labial palpus, lateral view.
Fig. 198. Male labium with left labial palpus, lateral view.

Tribe Ecitonini

Species examined:

- Eciton burchelli* (worker, soldier, male) (Plates 52–54)
E. drepanophorum (soldier)
E. dulcius (soldier)
E. dulcius crassinode (queen) (Plates 55, 56)
E. hamatum (soldier, queen) (queen, Plates 57, 58)
E. lucanoides (worker, soldier) (soldier, Plate 59)
E. mexicanum (worker, soldier, queen) (Plates 60–62)
E. quadriglume (worker, soldier) (soldier, Plates 63, 64)
E. rapax (major worker)
Labidus coecus (worker, soldier, queen) (soldier, Plate 65, queen, Plate 66)
L. praedator (worker, soldier) (soldier, Plate 67)
L. spininodis (worker)
Neivamyrmex agilis (major worker)
N. carolinensis (major worker)
N. gibbatus (major worker)
N. harrisi (male) (Plate 68)
N. humilis (major worker)
N. laevigatus (major worker)
N. legionis (major worker)
N. nigrescens (major worker, queen) (major worker, Plate 69)
N. opacithorax (major worker, queen)
N. pilosus (major worker)
N. postcarinatus (major worker)
N. sumichrasti (major worker) (Figs. 271–275)
N. swainsoni (male) (Plate 71)
N. wheeleri (major worker) (Fig. 276)
Nomamyrmex esenbecki (major and media workers) (major worker, Plate 72)
N. hartigi (major worker)

Labrum. The labrum of the Ecitonini is distinctly bilobed. The distal margin is always emarginate and usually has a median cleft. Labral tubercles are nearly always present in workers and soldiers, and when the tubercles are absent in these castes [*E. quadriglume* soldiers (fig. 242), *Nomamyrmex esenbecki* major worker (fig. 283)], they are present in the smaller workers of the same species. The labrum of *E. mexicanum* workers and soldiers is typical of most ecitonine labra of these castes (figs. 224, 229). Labral tubercles appear to be best developed and most prominent in the genus *Neivamyrmex*. They are either peglike or spinelike and are proportionately larger than in other genera. Tubercles are never present on the labra of sexual forms; the labrum of the queen of *E. mexicanum* (fig. 234) is typical of

sexual forms. The labral hemocoel of soldiers and workers consists of 2 arms, 1 in each lobe, which were not united medially in those examined. In queens and males, the hemocoel either occupies the entire labrum or it occupies it with the exception of a median strip which separates the hemocoel into 2 parts. The labrum is usually heavily sclerotized. This is particularly true for *Nomamyrmex* (fig. 283), in which the labrum is thick and bears a heavy ridge near and parallel to the distal margin. Generally the labra of males are more abundantly setose than others, and this is particularly true for *E. burchelli* (fig. 206). In *N. gibbatus* a median point projects out over the median cleft.

Mandible. The variation in shape of the mandible is great, not only between species, but between castes of a single species as well. The mandibles of *E. mexicanum* castes (figs. 227, 231, 235) are generally typical of the intraspecific variation that can occur. With the exception of *E. rapax*, which does not have a distinct soldier caste, the mandibles of *Eciton* soldiers are cylindrical and hooklike. These mandibles are sharply pointed apically and are usually without subapical teeth or irregularities, although *E. lucanoides* does possess a subapical tooth medially along the mandible's length (fig. 222). In the workers of *E. mexicanum*, the mandible is triangulate with an apical tooth and several subapical denticles or irregularities. In the queen the mandible is linear and slightly curved distally and is pointed apically but without subapical teeth. The mandibles of males of *Eciton* are usually similar to that of *E. burchelli* (fig. 205), but in other ecitonine genera, they are usually proportionately broader and more falcate [e.g. *Neivamyrmex swainsoni* (fig. 278)]. There is much less difference between the mandibles of workers and soldiers of *Labidus* than occurs in *Eciton*. The mandibles of ecitonine workers are triangulate but with varying dentition and some variation in the appearance of the basal and masticatory margins. The mandibles of the *Neivamyrmex* species examined can be categorized into three groups: one in which the basal margin curves smoothly into the masticatory margin; another in which the basal margin is abruptly shouldered, forming a subquadrate bulge along the internal margin; and another in which the mandible is truncated apically and the basal margin is long and convex. To the first type belong *N. gibbatus*, *humilis*, *laevigatus*, *legionis*, *nigrescens* (fig. 266), *pilosus*, and *sumachrasti*; to the second *N. agilis*, *carolinensis*, *opacithorax*, and *wheeleri*; and to the third *N. postcarinatus*. Mandibular setal patterns and abundance vary widely among ecitonines. While the mandalus appears to be present in all the mandibles examined, the trulleum is often absent or modified in the mandibles of soldiers, queens, and males.

Maxilla. The maxillary palpus is 2-segmented in all species and castes examined. The stipites of soldiers and workers are relatively uniform in shape and construction throughout the Ecitonini. The stipes of the soldier

of *E. burchelli* is typical (fig. 203). The lateral shoulder is strongly developed and usually bears numerous long setae, although these setae are very short in *Labidus praedator* (fig. 256) and *spininodis*. The transverse stiptal groove is also strongly developed, and the proximal external face bears from several to many setae. The stipes of the queen of *E. mexicanum* (fig. 237) is typical of most queens and males of all genera except *Neivamyrmex*. The lateral shoulder is heavily setose, and the transverse groove absent, although a distinct impression extends diagonally across the stipes in its place. In the sexual forms of *Neivamyrmex* (figs. 263, 280), the transverse groove is not lost and remains strongly developed. Here also setae are more abundant in the queens and males than in the workers. This is particularly true for the stipes of *Neivamyrmex swainsoni* (fig. 280). The stiptes of ecitonines are usually heavily sclerotized. The galea and lacinia of the soldier of *E. burchelli* (fig. 202) is typical of soldiers and workers. The galeal crown is flattened, and bears numerous long setae; the galeal comb is exceptionally well developed and comprises as many as 8 or 9 large, uniquely shaped setae. This galea is also fairly typical of that of queens and males which also have a well developed galeal comb. The galeal comb is lacking in only one caste, the male of *Neivamyrmex swainsoni* (fig. 279). The lacinia is triangular in shape in all species and castes and bears a prominent comb. This comb is always distinct and continuous in soldiers and workers and always discontinuous (i.e. major gaps occur at points along the comb separating the setae into distinct groups) in queens and males. The lacinial gonion does not bear any setae.

Labium. The labial palpus is 3-segmented in all soldiers and workers of *Eciton*, *Labidus*, and *Nomamyrmex* and 2- or 3-segmented in the workers of *Neivamyrmex*. Among the queens and males examined in all genera, the labial palpus is 2-segmented. Those *Neivamyrmex* workers having a 2-segmented palpus are *agilis*, *carolinensis*, *humilis*, *opacithorax*, and *wheeleri*. The premental shield appears to be moderately sclerotized and the epimental sclerites are relatively distinct. The labium of the soldier of *E. quadriglume* (fig. 240) demonstrates the general structure of the ecitonine labium. It would appear that the raquettes are well developed in this species, but these structures are not distal expansions of the epimental sclerites. They appear in no other species. The subglossal brushes are prominent and the included setae are sometimes enlarged apically. Both paraglossae and paraglossal sensory pegs are absent throughout the tribe.

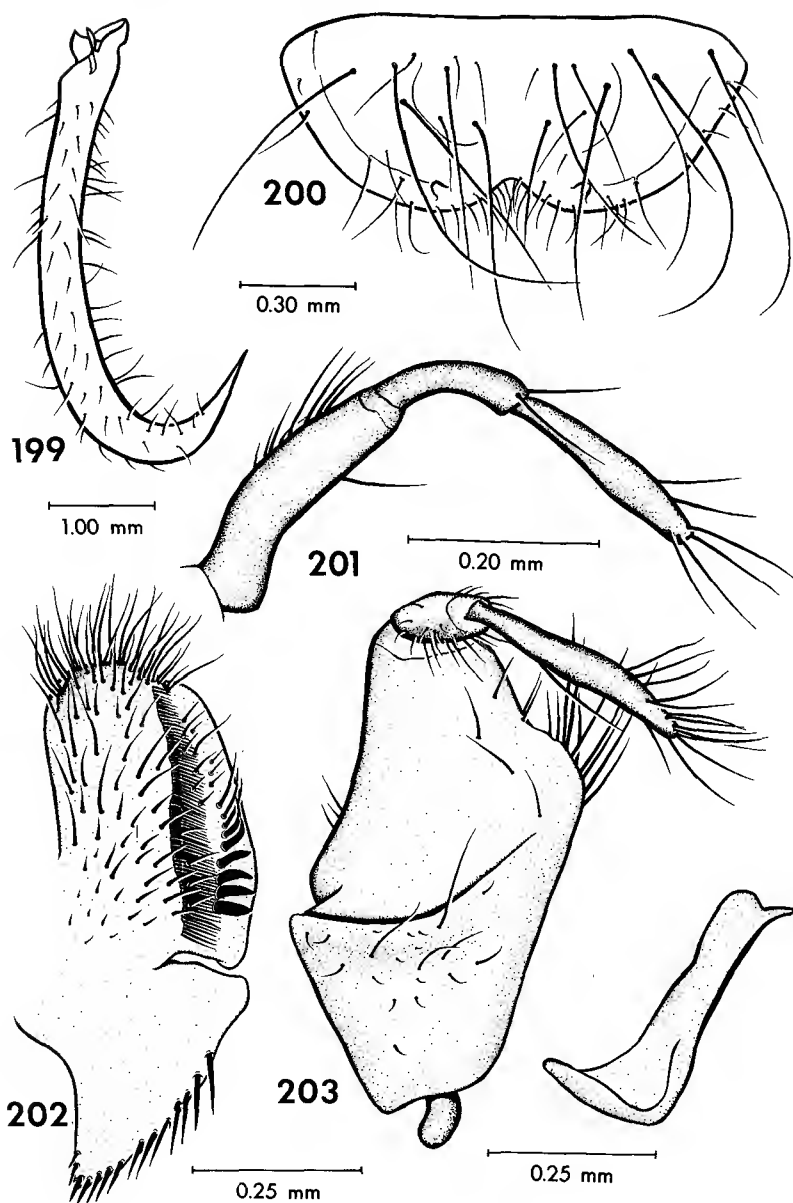


Plate 52. *Eciton burchelli* (soldier).

- Fig. 199. Right mandible, dorsal view.
 Fig. 200. Labrum, external view.
 Fig. 201. Right labial palpus, lateral view.
 Fig. 202. Left galea and lacinia, external view.
 Fig. 203. Left stipes, maxillary palpus, and cardo, external view.

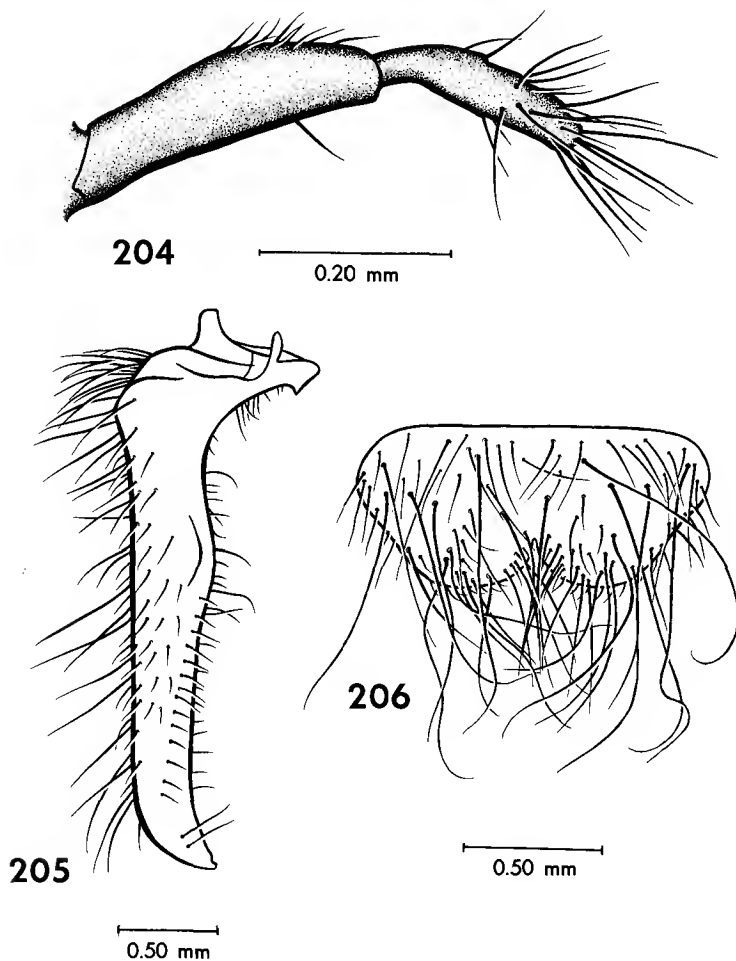


Plate 53. *Eciton burchelli* (male).

Fig. 204. Right labial palpus, lateral view.

Fig. 205. Right mandible, dorsal view.

Fig. 206. Labrum, external view.

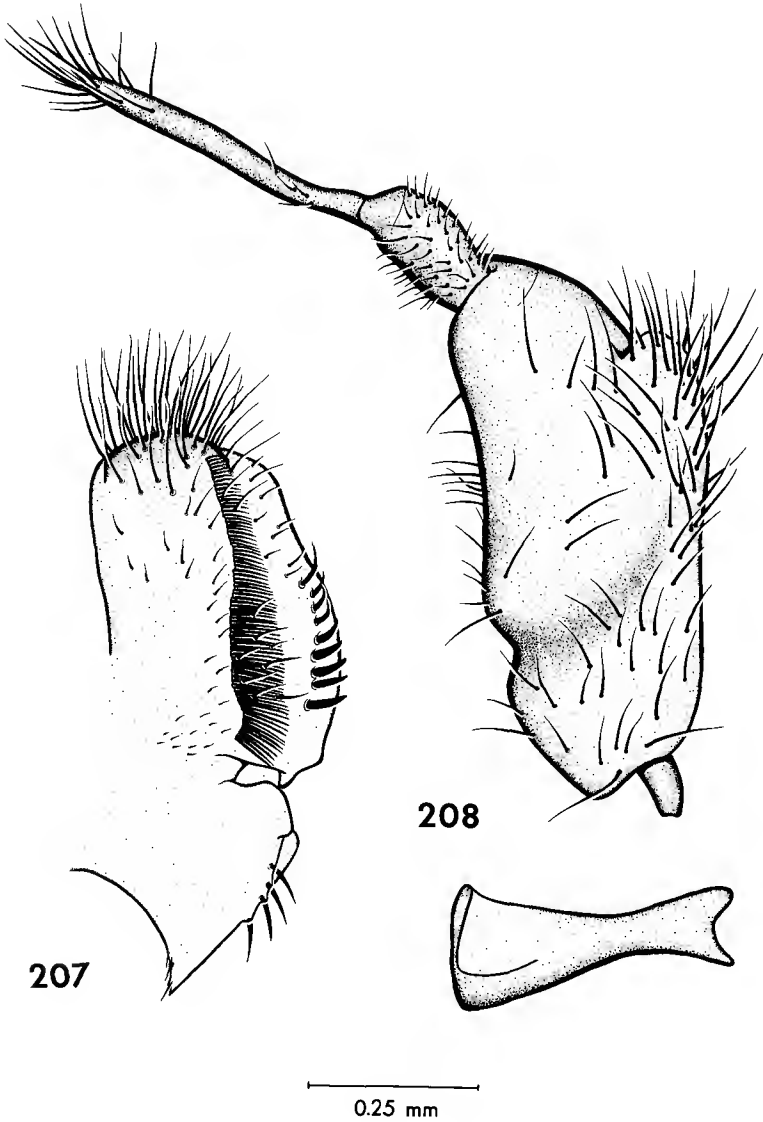


Plate 54. *Eciton burchelli* (male).

Fig. 207. Left galea and lacinia, external view.

Fig. 208. Left stipes, maxillary palpus, and cardo, external view.

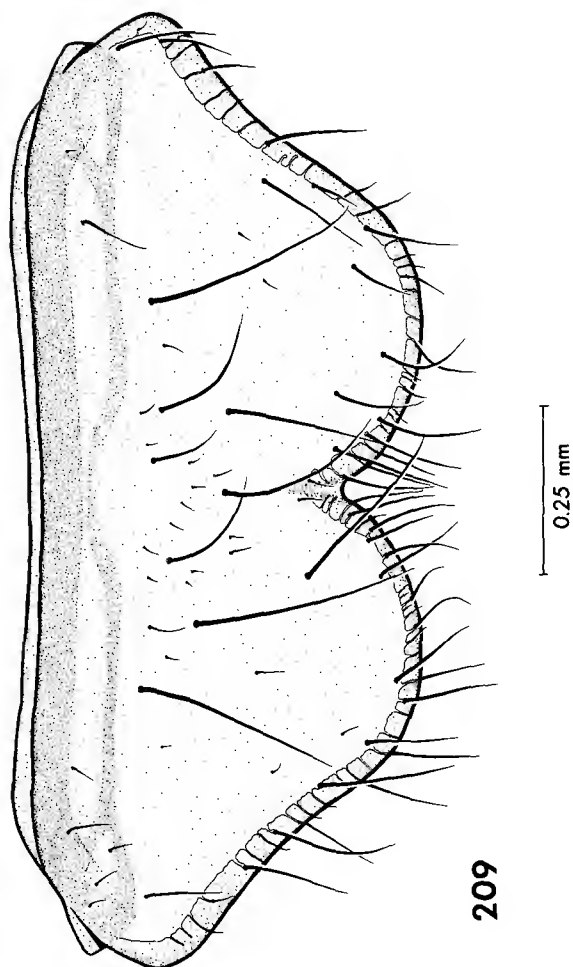


Plate 55. *Eciton dulcius crassinode* (queen).

Fig. 209. Labrum, external view.

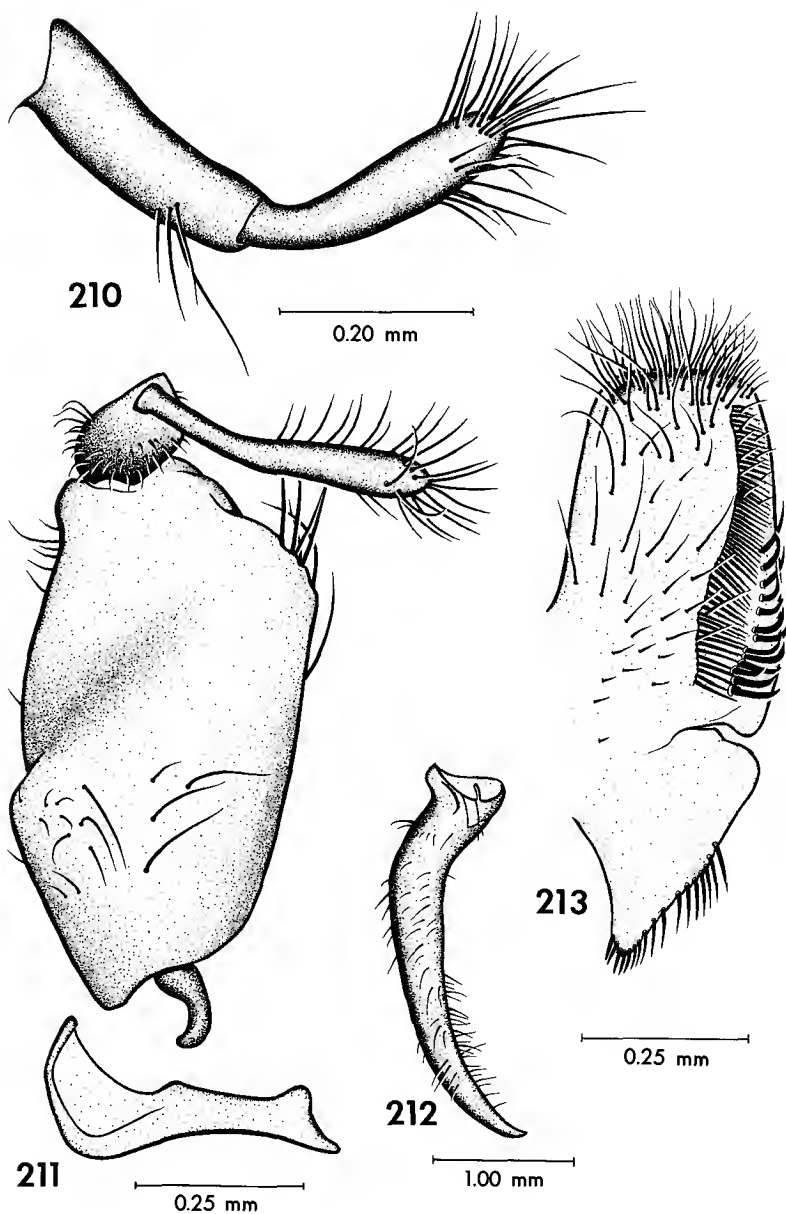


Plate 56. *Eciton dulcius crassinode* (queen).

- Fig. 210. Right labial palpus, lateral view.
Fig. 211. Left stipes, maxillary palpus, and cardo, external view.
Fig. 212. Right mandible, dorsal view.
Fig. 213. Left galea and lacinia, external view.

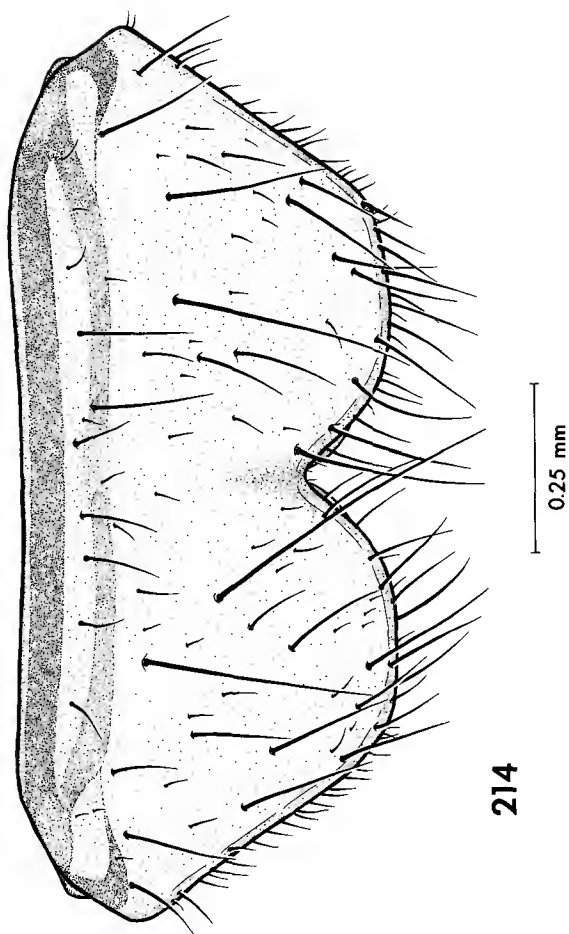


Plate 57. *Eciton hamatum* (queen).

Fig. 214. Labrum, external view.

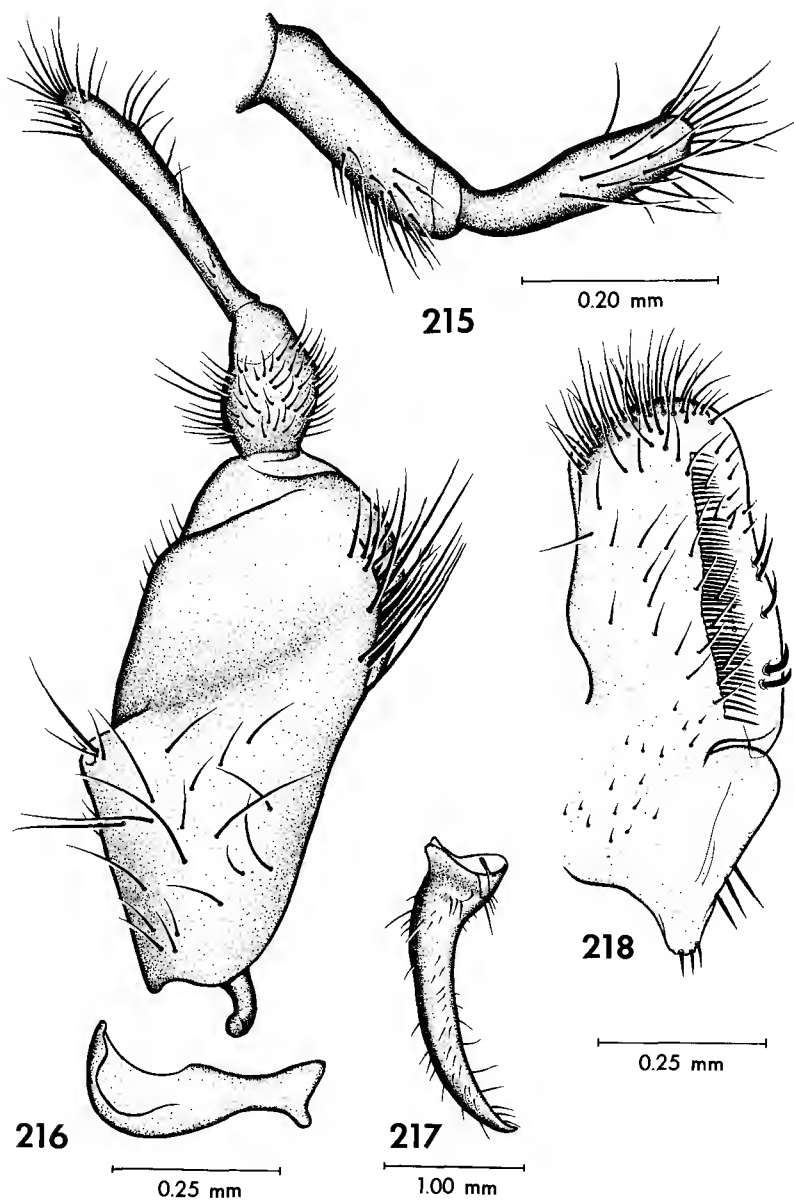


Plate 58. *Eciton hamatum* (queen).

- Fig. 215. Right labial palpus, lateral view.
 Fig. 216. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 217. Right mandible, dorsal view.
 Fig. 218. Left galea and lacinia, external view.

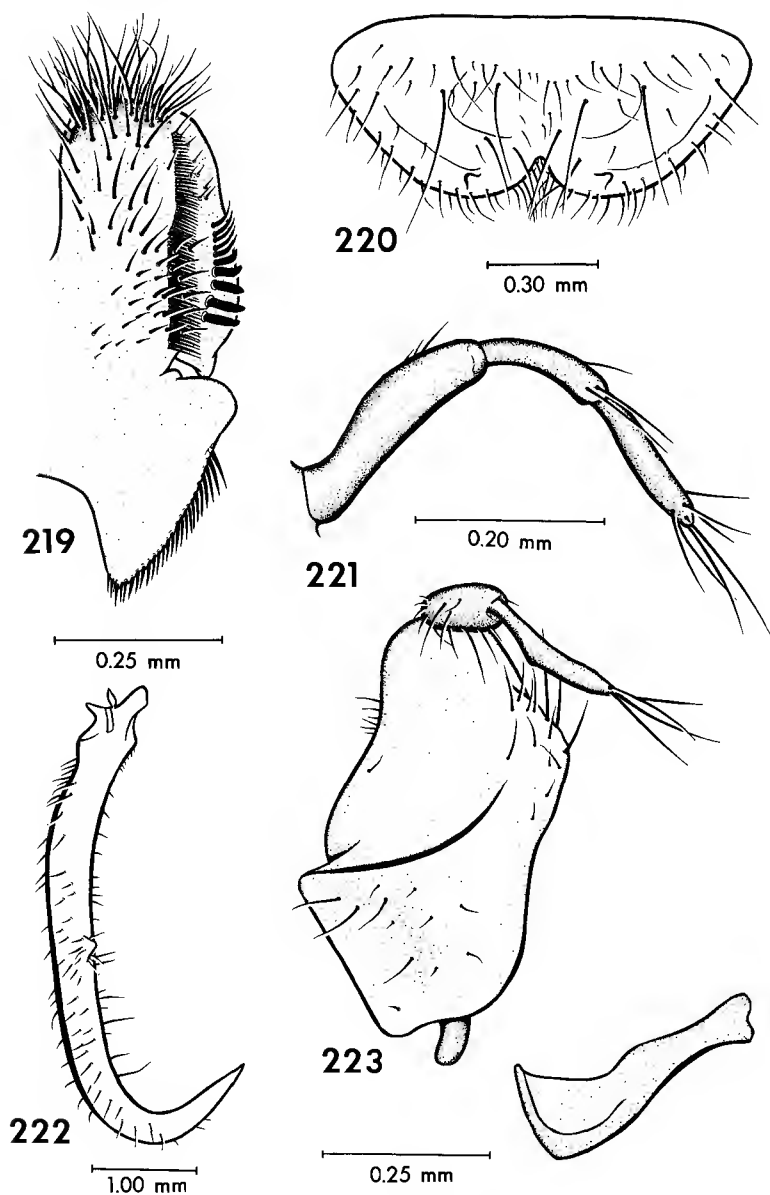


Plate 59. *Eciton lucanoides* (soldier).

- Fig. 219. Left galea and lacinia, external view.
 Fig. 220. Labrum, external view.
 Fig. 221. Right labial palpus, lateral view.
 Fig. 222. Right mandible, dorsal view.
 Fig. 223. Left stipes, maxillary palpus, and cardo, external view.

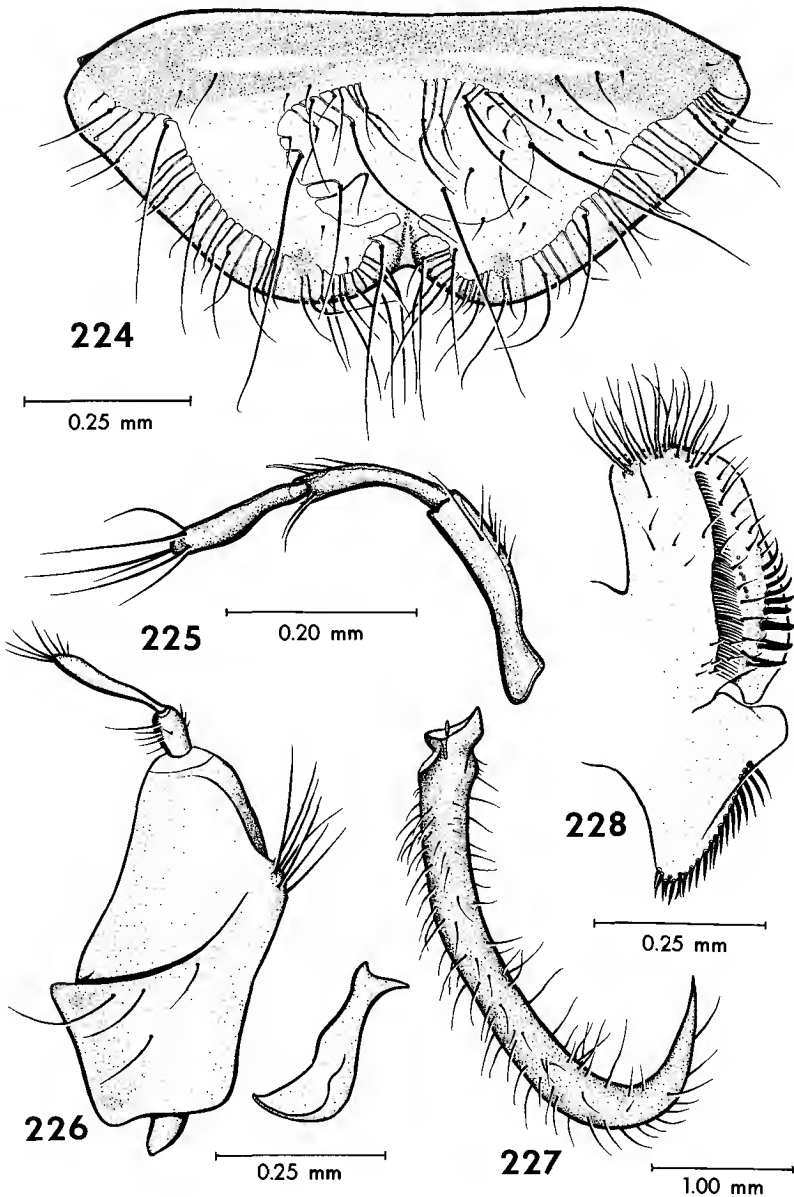


Plate 60. *Eciton mexicanum* (soldier).

- Fig. 224. Labrum, external view.
 Fig. 225. Left labial palpus, lateral view.
 Fig. 226. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 227. Right mandible, dorsal view.
 Fig. 228. Left galea and lacinia, external view.

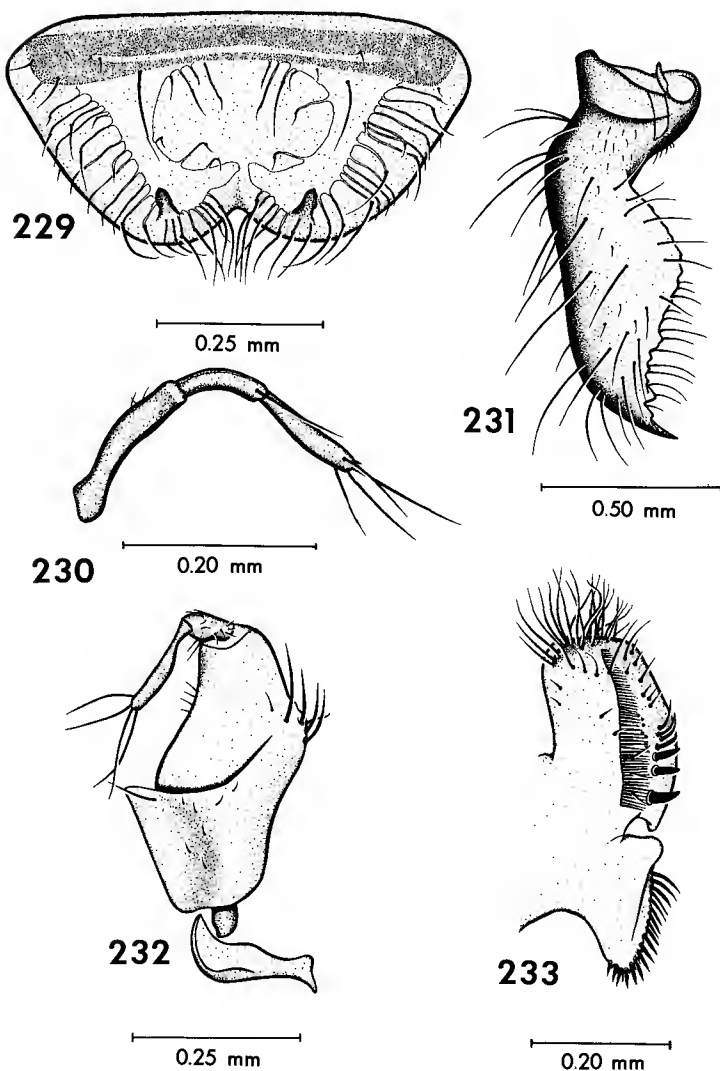


Plate 61. *Eciton mexicanum* (worker).

- Fig. 229. Labrum, external view.
 Fig. 230. Right labial palpus, lateral view.
 Fig. 231. Right mandible, dorsal view.
 Fig. 232. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 233. Left galea and lacinia, external view.

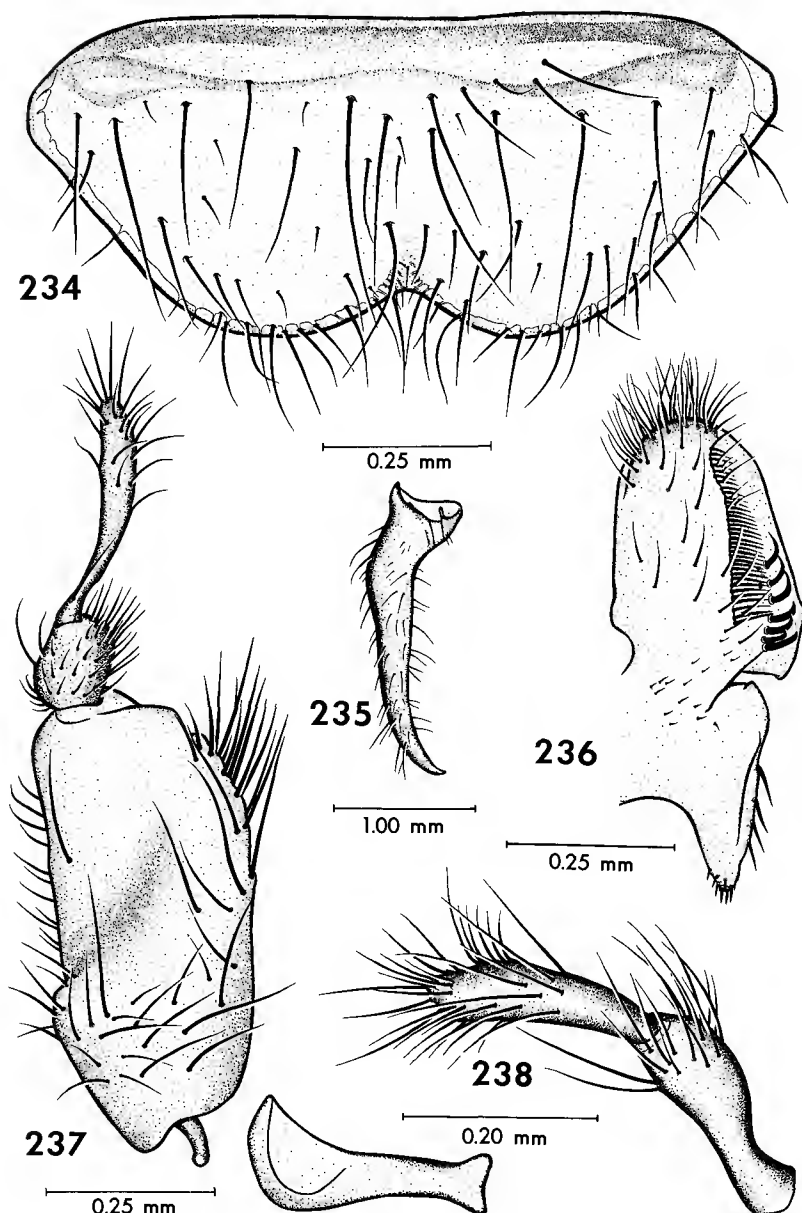


Plate 62. *Eciton mexicanum* (queen).

- Fig. 234. Labrum, external view.
 Fig. 235. Right mandible, dorsal view.
 Fig. 236. Left galea and lacinia, external view.
 Fig. 237. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 238. Left labial palpus, lateral view.

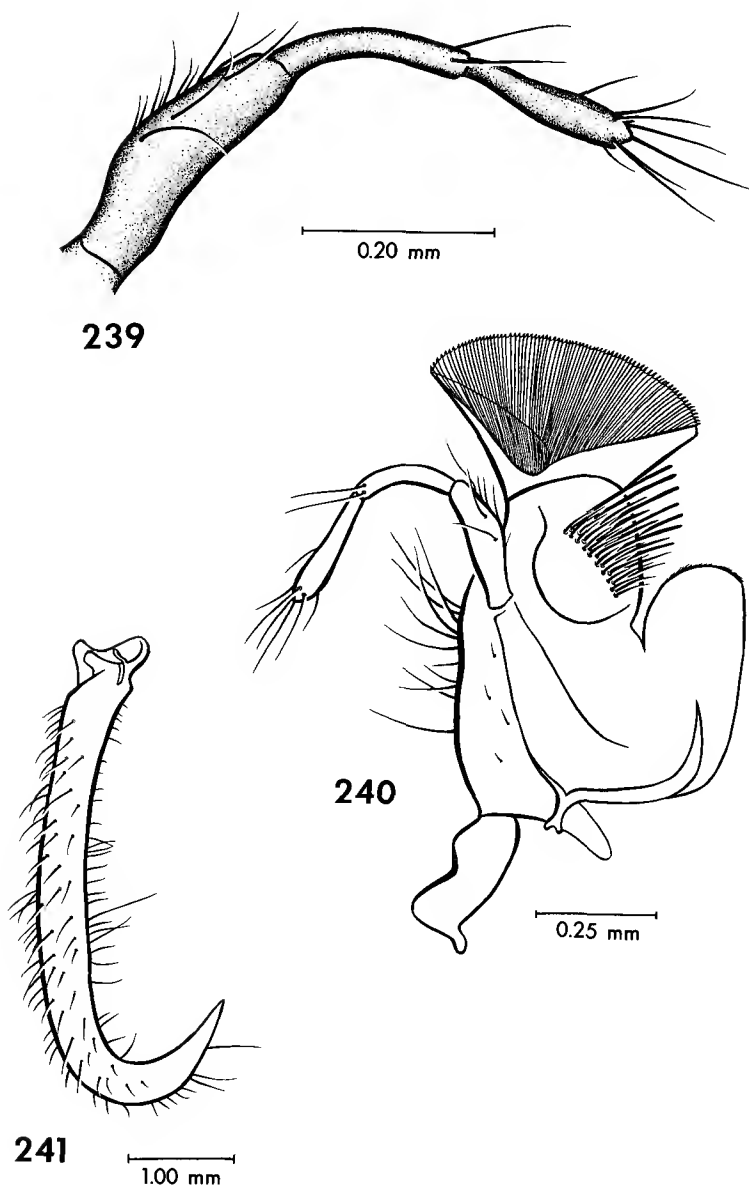


Plate 63. *Eciton quadriglume* (soldier).

Fig. 239. Right labial palpus, lateral view.

Fig. 240. Labium with left labial palpus, lateral view.

Fig. 241. Right mandible, dorsal view.

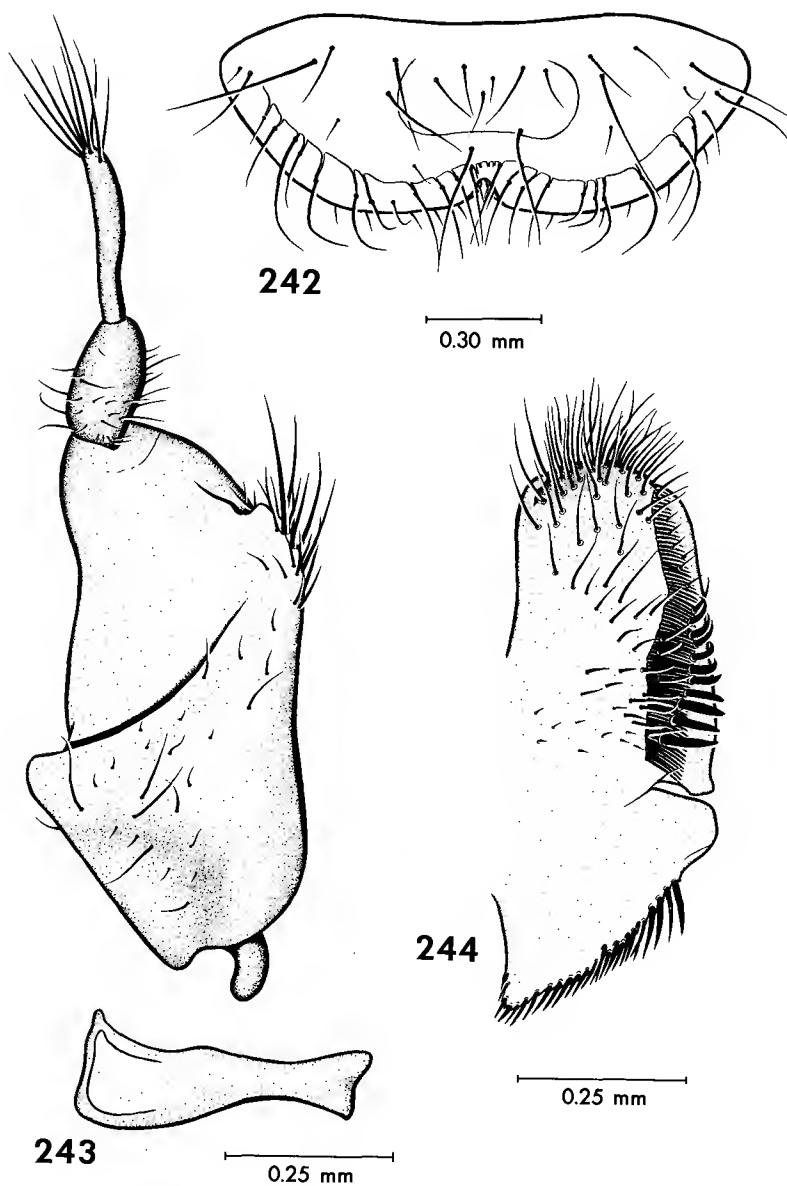
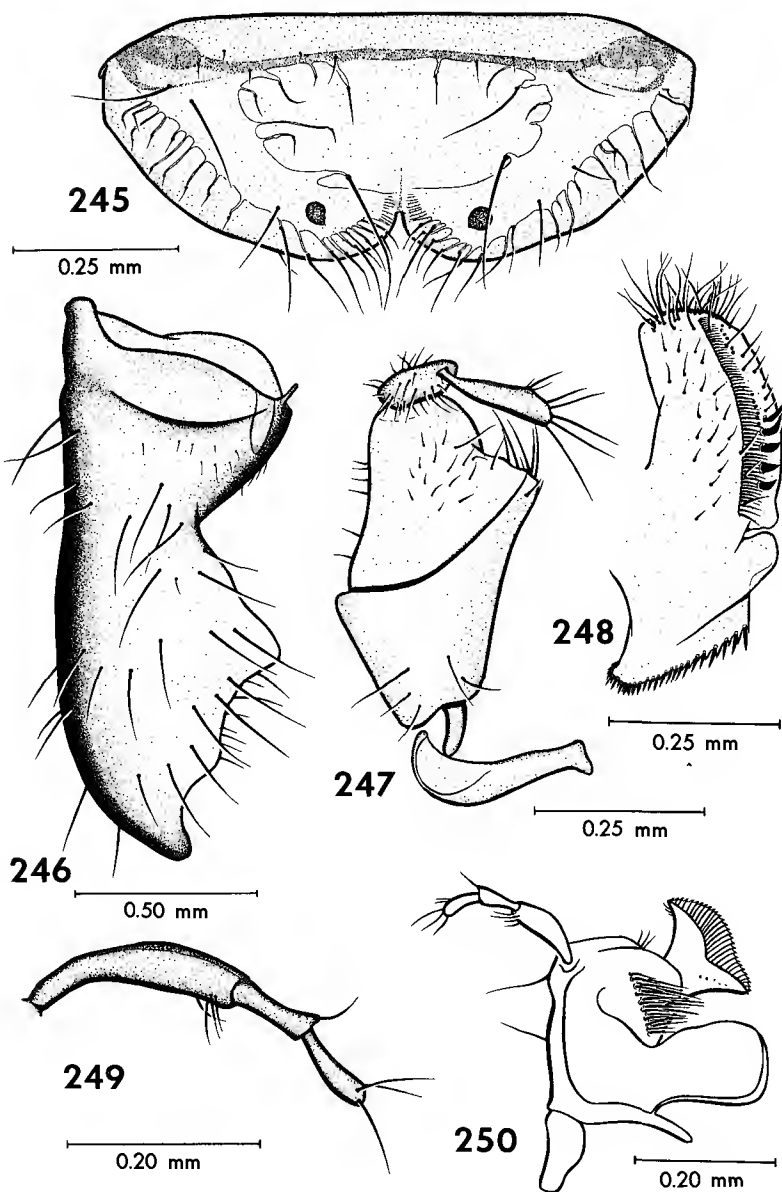


Plate 64. *Eciton quadriglume* (soldier).

Fig. 242. Labrum, external view.

Fig. 243. Left stipes, maxillary palpus, and cardo, external view.

Fig. 244. Left galea and lacinia, external view.

Plate 65. *Labidus coecus* (soldier).

- Fig. 245. Labrum, external view.
 Fig. 246. Right mandible, dorsal view.
 Fig. 247. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 248. Left galea and lacinia, external view.
 Fig. 249. Right labial palpus, lateral view.
 Fig. 250. Labium with left labial palpus, lateral view.

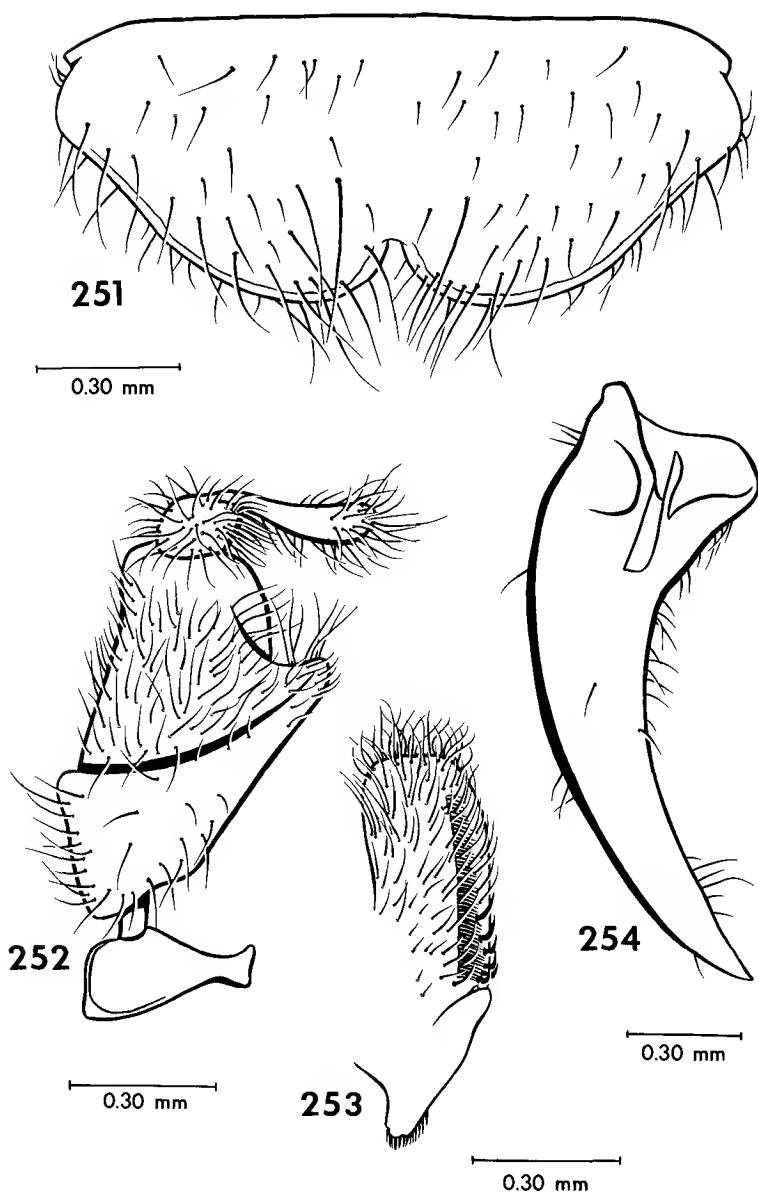


Plate 66. *Labidus coecus* (queen).

Fig. 251. Labrum, external view.

Fig. 252. Left stipes, maxillary palpus, and cardo, external view.

Fig. 253. Left galea and lacinia, external view.

Fig. 254. Right mandible, dorsal view.

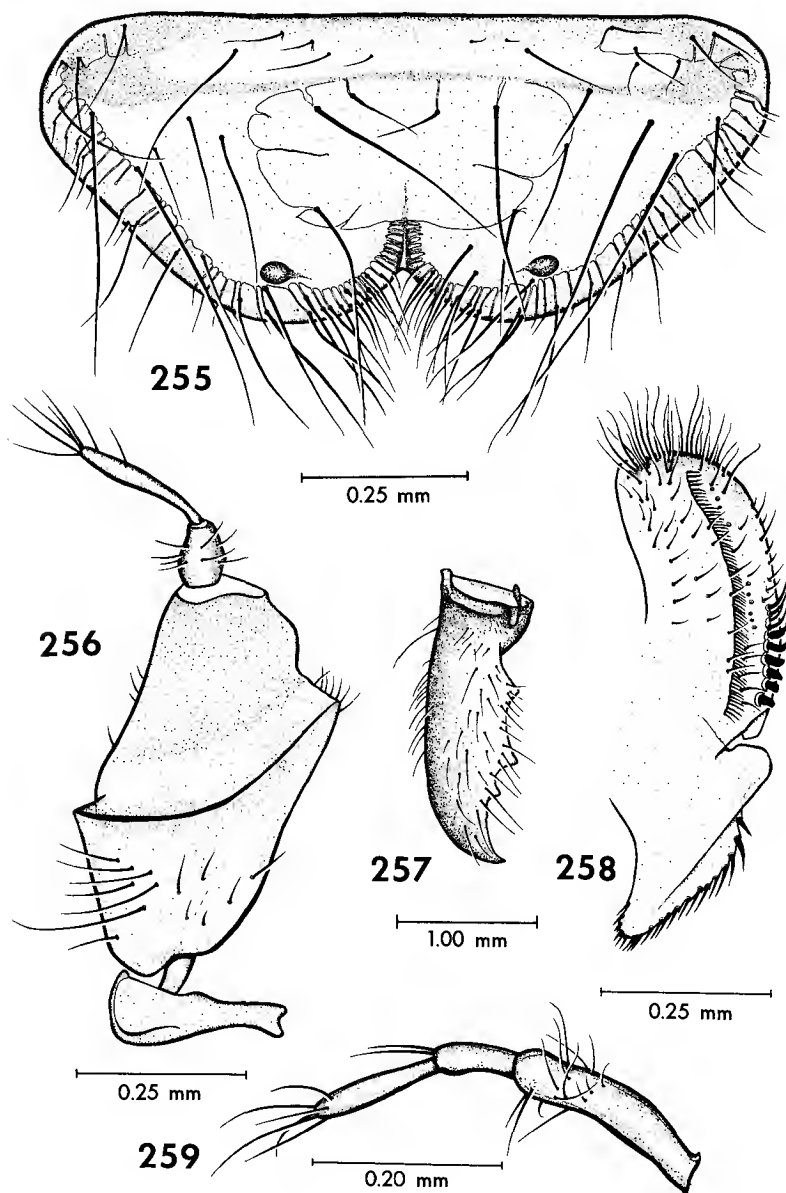


Plate 67. *Labidus praedator* (soldier).

- Fig. 255. Labrum, external view.
 Fig. 256. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 257. Right mandible, dorsal view.
 Fig. 258. Left galea and lacinia, external view.
 Fig. 259. Left labial palpus, lateral view.

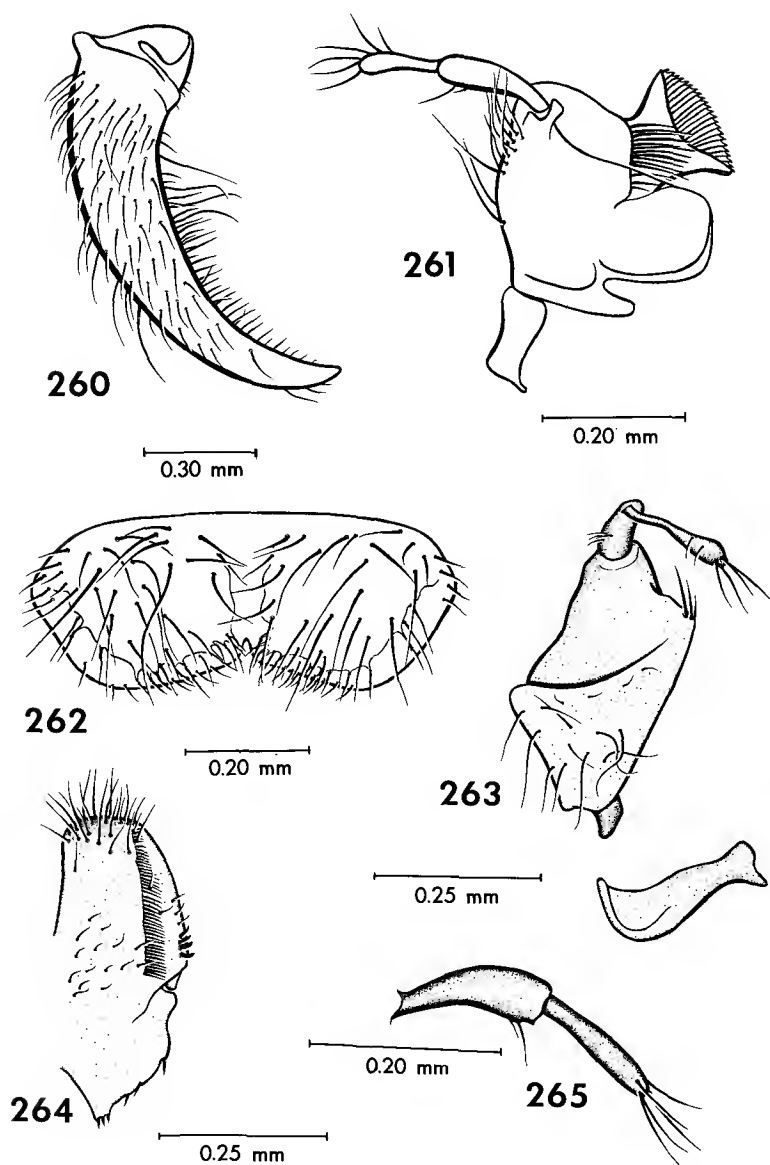


Plate 68. *Neivamyrmex harrisi* (male).

- Fig. 260. Right mandible, dorsal view.
 Fig. 261. Labium with left labial palpus, lateral view.
 Fig. 262. Labrum, external view.
 Fig. 263. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 264. Left galea and lacinia, external view.
 Fig. 265. Right labial palpus, lateral view.

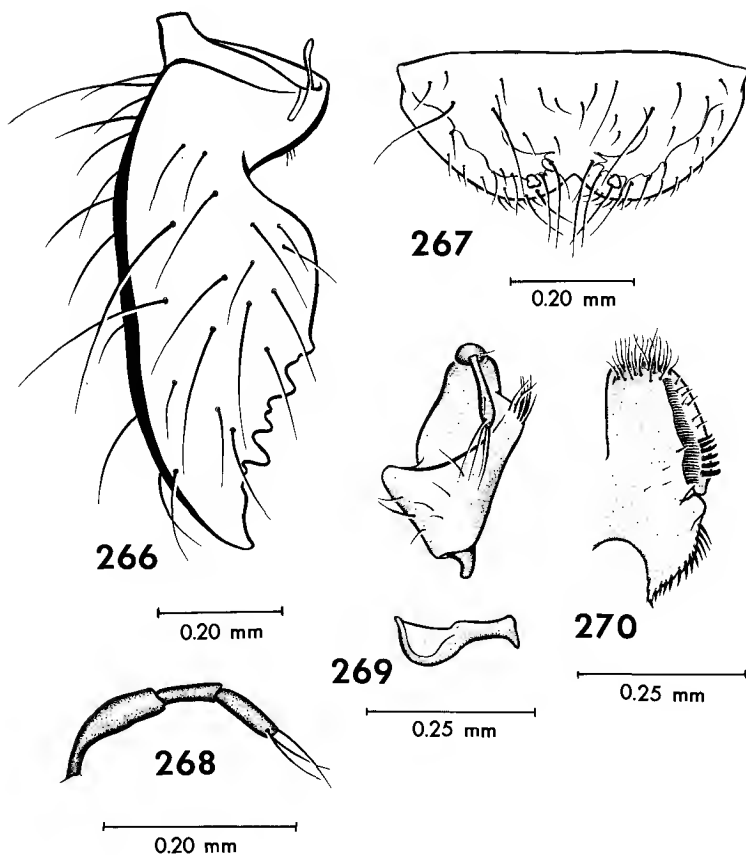


Plate 69. *Neivamyrmex nigrescens* (worker).

Fig. 266. Right mandible, dorsal view.

Fig. 267. Labrum, external view.

Fig. 268. Right labial palpus, lateral view.

Fig. 269. Left stipes, maxillary palpus, and cardo, external view.

Fig. 270. Left galea and lacinia, external view.

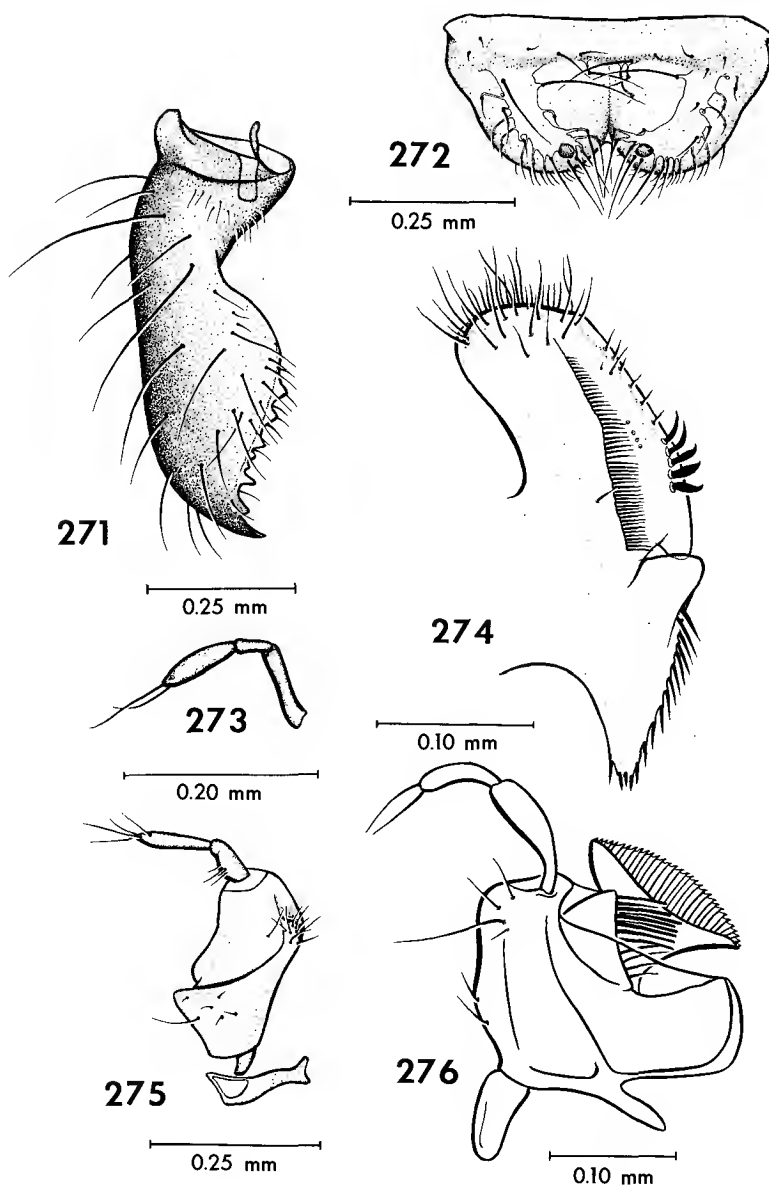


Plate 70.

- Fig. 271. Right mandible of *Neivamyrmex sumichrasti*, dorsal view.
 Fig. 272. Labrum of *N. sumichrasti*, external view.
 Fig. 273. Left labial palpus of *N. sumichrasti*, lateral view.
 Fig. 274. Left galea and lacinia of *N. sumichrasti*, external view.
 Fig. 275. Left stipes, maxillary palpus and cardo of *N. sumichrasti*, external view.
 Fig. 276. Labium with left labial palpus of *N. wheeleri*, lateral view.

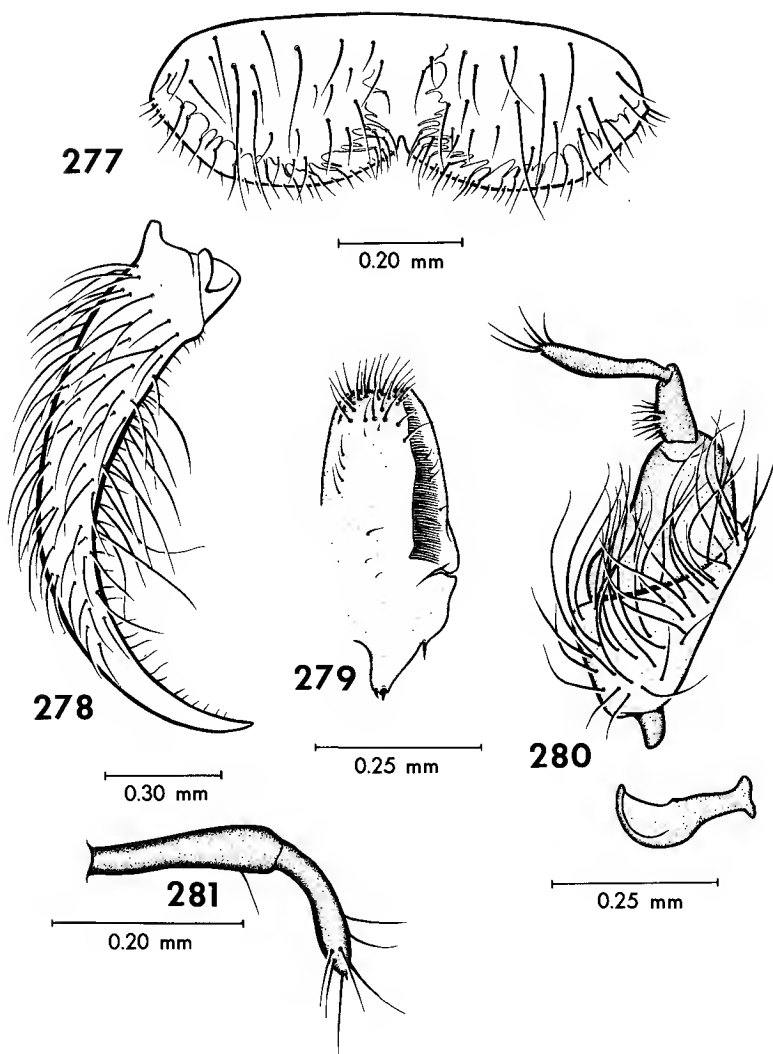


Plate 71. *Neivamyrmex swainsoni* (male).

- Fig. 277. Labrum, external view.
 Fig. 278. Right mandible, dorsal view.
 Fig. 279. Left galca and lacinia, external view.
 Fig. 280. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 281. Right labial palpus, lateral view.

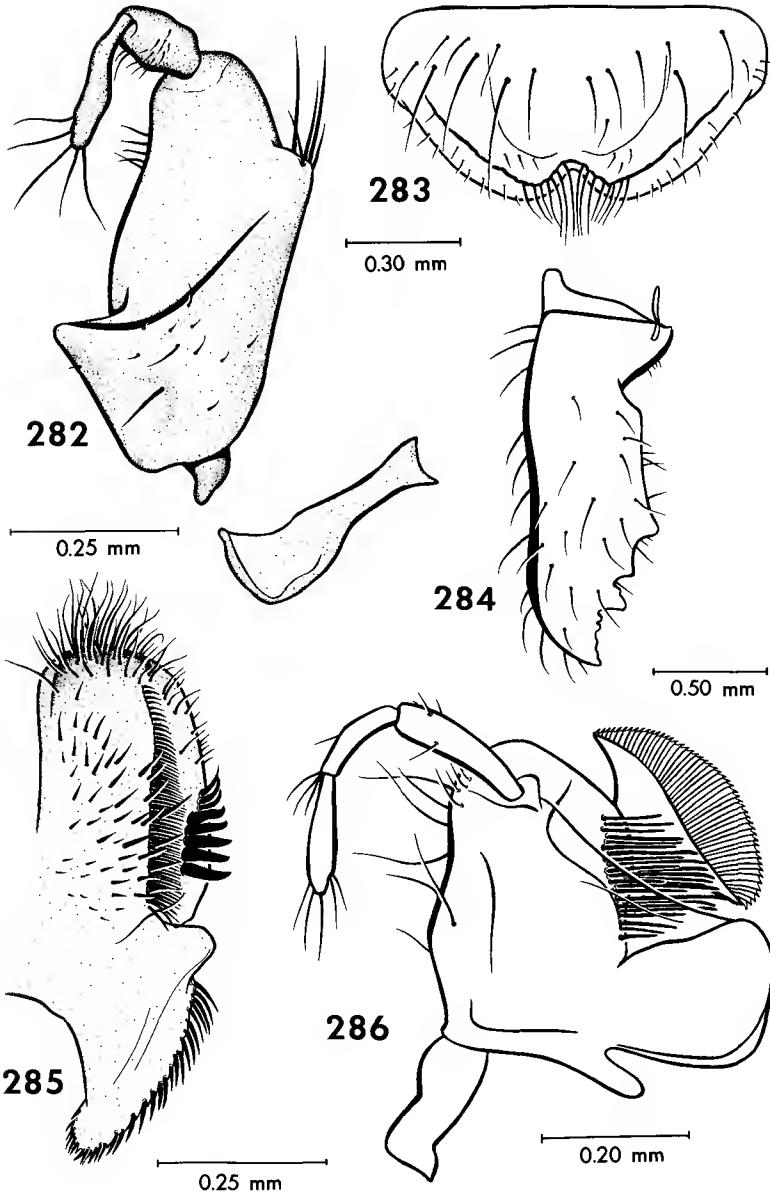


Plate 72. *Nomamyrmex esenbecki* (worker).

- Fig. 282. Left stipes, maxillary palpus and cardo, external view.
 Fig. 283. Labrum, external view.
 Fig. 284. Right mandible, dorsal view.
 Fig. 285. Left galea and lacinia, external view.
 Fig. 286. Labium with left labial palpus, lateral view.

Subfamily Leptanillinae

Species examined:

Phaulomyrma javana (male, holotype) (Fig. 287)

By necessity the mouthparts of *P. javana* were examined in situ. The head, thorax, and abdomen of the type specimen are mounted on glass slides, making it impossible to manipulate the trophi, and thus the galea, lacinia, and labrum are wholly or partially obscured from view. Kutter (1948) figured the mouthparts of *Leptomesites escheri* and discussed palpal segmentation for the subfamily. This paper, as well as the original description of *Phaulomyrma javana* (Wheeler and Wheeler, 1930), are referred to here to better reflect an overall view of the subfamily.

Labrum. The labrum of *P. javana* could not be seen, nor was it discussed by Wheeler and Wheeler (1930), and that of *L. escheri* was not discussed or figured by Kutter (1948).

Mandible. The mandible of *P. javana* is short, rounded, and can probably be regarded as toothless. Kutter (1948) described the male mandible for the entire subfamily similarly. For *L. escheri*, Kutter described the worker mandible as having 3 teeth and the queen mandible as acuminate and with a narrow masticatory margin, finely toothed or crenated. The condition of the trulleum and mandalus is unknown.

Maxilla. The maxillary palpus of the *P. javana* male is 1-segmented (fig. 287). This palpus is 2-segmented in the worker of *L. escheri* (Kutter, 1948). The stipes of the male of *P. javana* is without a transverse groove and without setae on the lateral shoulder (fig. 287). The proximal external face has 3 long setae. Although a portion of the galea of *P. javana* is visible, its shape or structure could not be ascertained. The lacinia of this species was not observable on the specimen examined. There is a similar lack of detail for *L. escheri* in Kutter's description and drawing.

Labium. The labial palpus of the male of *P. javana* (fig. 287) is 1-segmented, as is that of the worker of *L. escheri* (Kutter, 1948). According to Wheeler and Wheeler (1930) and Kutter (1948), the labial palpus is 1-segmented throughout the subfamily in all castes. A lateral view of the labium of *P. javana* was not possible, and no conclusions can be drawn regarding the epimental sclerites, subglossal brushes, and paraglossae. The labium of *L. escheri* was not figured laterally by Kutter.

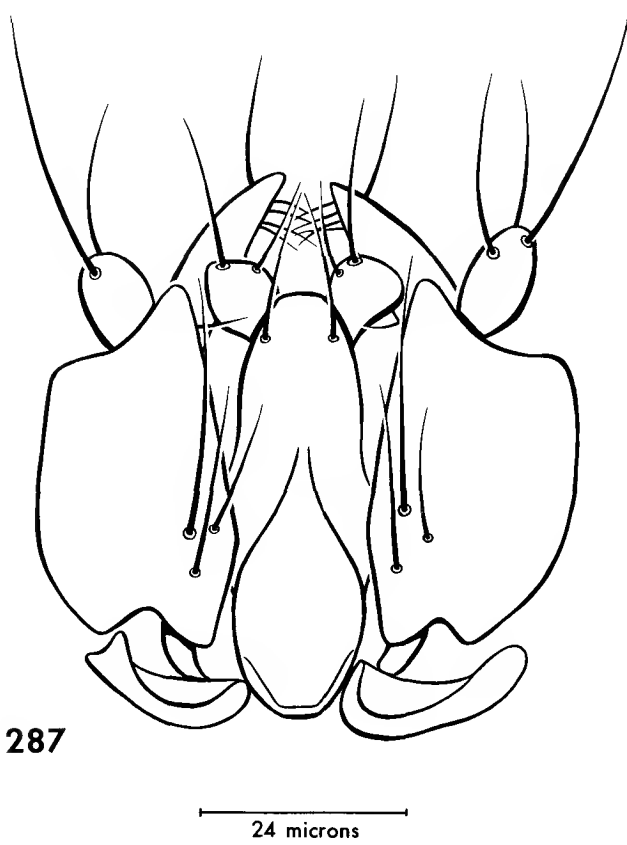


Plate 73. *Phaulomyrma javana* (male).

Fig. 287. Maxillo-labial apparatus in situ, ventral view.

Subfamily Myrmicinae

Species examined:

Adelomyrmex tristani (Plate 74)*Aphaenogaster rudis**Apterostigma gibbum* (Plate 75)*Blepharidatta brasiliensis*

(Plate 76)

Crematogaster cf. *brasiliensis**Cyphomyrmex rimosus* complex

(Plate 77)

Daceton armigerum (Plate 78)*Lachnomyrmex scrobiculatus*

(Plate 79)

Melissotarsus beccarii (queen)*Meranoplus dichrous**Messor barbarus**Metapone truki* (Plate 80)*Ocymyrmex barbiger* (Plate 81)*Pheidole desertorum* (soldier)*Pogonomyrmex estebaninus*

(Plate 82)

*Solenopsis texana**Tetramorium pacificum**Vollenhovia* n. sp. (Plate 83)*Wasmannia auropunctata*

(Plate 84)

Labrum. The labrum is always at least emarginate medially along the distal margin and is usually also cleft. The shape of the labrum most commonly resembles that of *Pogonomyrmex estebaninus* (fig. 323), although it radically departs from this example in *Daceton armigerum* (fig. 304), *Metapone truki* (fig. 314), and *Melissotarsus beccarii*. In all species examined, the hemocoel consists of 2 arms, 1 in each lobe of the labrum, which usually do not unite medially. Again *Metapone* is an exception with its hemocoel arms united narrowly across the middle of the labrum. Other species have these arms united anteriorly [*Adelomyrmex tristani* (fig. 290), *Aphaenogaster rudis*, *Messor barbarus*, and *Pheidole desertorum*]. The large labral setae of *Metapone truki* (fig. 314) are placed at the distal lateral angles of the labrum. Labral tubercles are lacking in the species examined.

Mandible. The mandible is most commonly triangular with well defined masticatory and basal margins as in *Vollenhovia* n. sp. (fig. 325). The mandible of *Daceton armigerum* (fig. 305) departs most radically from the triangular type. Other departures in shape exist in *Cyphomyrmex* sp. (fig. 302), *Metapone truki* (fig. 313), and *Ocymyrmex barbiger* (fig. 319). Among the triangular mandibles, there are usually from 3 to 5 subapical teeth or numerous denticles. Setae vary in abundance and size throughout the subfamily, and the trulleum and mandalus always appear to be present.

Maxilla. The maxillary palpus ranges from 1 segment in *Adelomyrmex tristani* (fig. 288) and *Solenopsis texana* to 6 segments in the queen of *Melissotarsus*. The stipes is relatively uniform in shape throughout the subfamily, usually subrectangular without a pronounced lateral shoulder. Although no species has a transverse stipital groove, *Blepharidatta brasiliensis* (fig. 296), *Tetramorium pacificum*, and *Wasmannia auropunctata*

(fig. 330) have a crescent-shaped groove distally near the palpal insertion. In these 3 species the maxillary palpus is 3-segmented and the shape of the stipes is quite similar. Also forming a group with respect to stipes shape and palpal segmentation are *Aphaenogaster rudis*, *Daceton armigerum* (fig. 306), *Meranoplus dichrous*, and *Messor barbarus*. The number of setae on the external surface varies throughout the group, but usually is low. The stipes of *Metapone truki* (fig. 315) bears a stout seta proximally, and that of *Ocymyrmex barbiger* (fig. 318) bears 2 exceptionally long setae near the proximal margin. The lateral shoulder never has conspicuous setae as in the Dorylinae. The galea of *Pogonomyrmex estebanius* (fig. 322) is typical of most myrmicine ants. It is subrectangular with a flattened galeal crown and no galeal comb. The galeal crown bears numerous setae, often including a row of stout setae forming a comb near and along the crown. *Apterostigma gibbum* (fig. 291) and *Metapone truki* (fig. 315) have setae arranged to approximate the galeal comb. In *Apterostigma*, however, these setae do not resemble the ecitonine type, although in *Metapone*, at least, these setae are stout. The lacinia is typically triangular as in *Pogonomyrmex estebanius* (fig. 322), but it does vary and is actually subquadrate in *Ocymyrmex barbiger* (fig. 320). The lacinial comb is composed of small setae and is sometimes inconspicuous. It is continuous in all species except *Ocymyrmex barbiger*, in which the setae are irregularly scattered along the lacinial margin. The lacinial gonion is without setae.

Labium. The labial palpi are commonly 2- or 3-segmented, but have 4 segments in the queen of *Melissotarsus beccarii*. The premental shield is moderately sclerotized, and the epimental sclerites, while always present, are often poorly defined. Raquettes are not evident. The subglossal brushes are always present. Highly developed among the myrmicines are the paired paraglossae. Each paraglossa is provided with a single sensory peg at its distal end (figs. 334-341). The shape of the paraglossae varies widely, and setae are usually inserted ventrad to the sensory peg. Paraglossae were found in all myrmicines examined except *Metapone truki* and (the queen of) *Melissotarsus beccarii*. Solitary sensory pegs are also absent in these last 2 species. The paraglossae are highly membranous and quite difficult to discern. They are typically located near the base of the glossa diagonally distad to the insertion of the subglossal brushes (e.g., as in fig. 294).

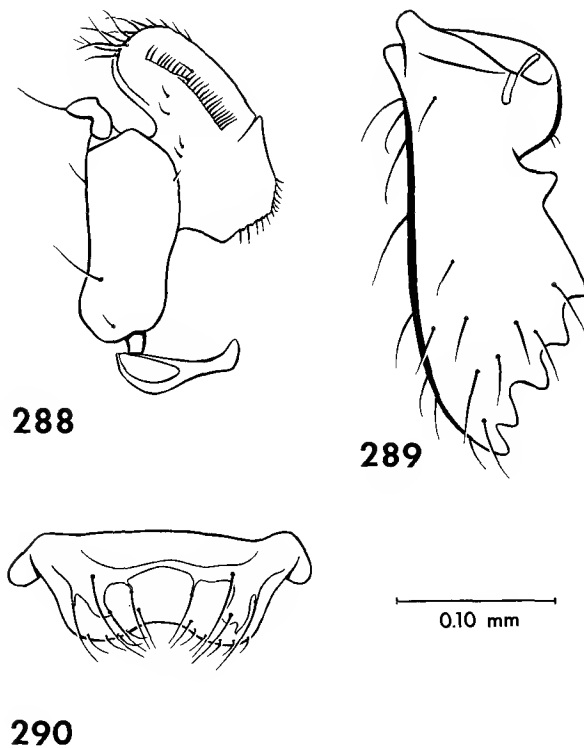


Plate 74. *Adelomyrmex tristani* (worker).

Fig. 288. Left maxilla, external view.

Fig. 289. Right mandible, dorsal view.

Fig. 290. Labrum, external view.

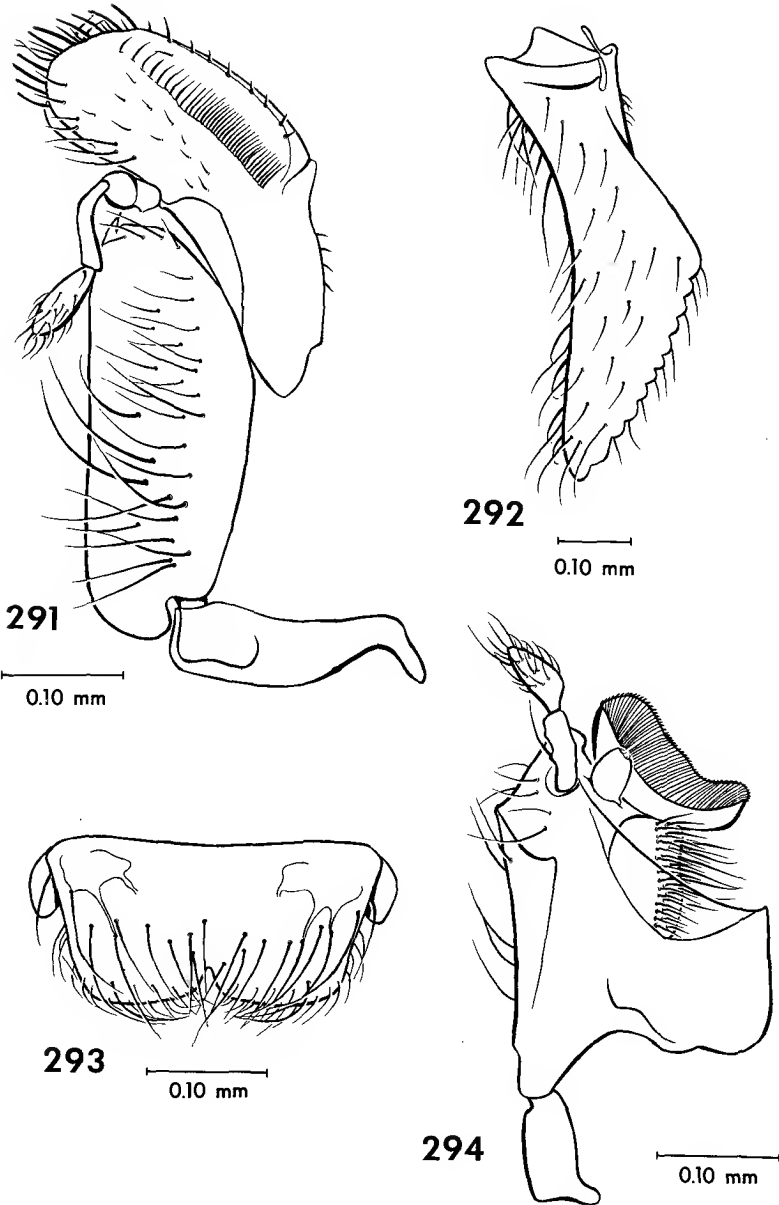


Plate 75. *Apterostigma gibbum* (worker).

Fig. 291. Left maxilla, external view.

Fig. 292. Right mandible, dorsal view.

Fig. 293. Labrum, external view.

Fig. 294. Labium with left labial palpus, lateral view.

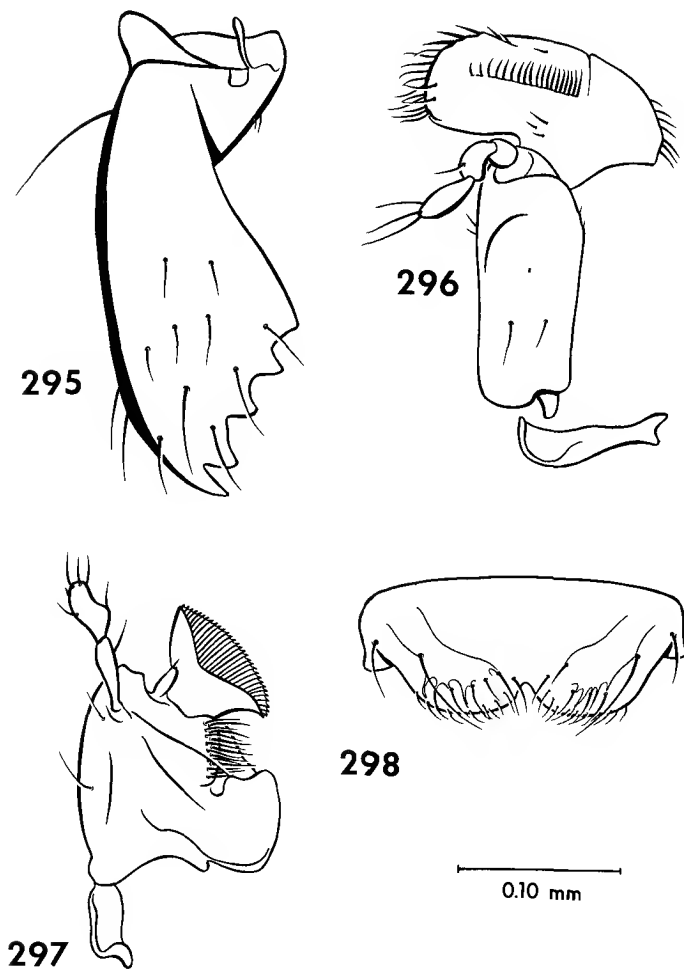


Plate 76. *Blepharidatta brasiliensis* (worker).

Fig. 295. Right mandible, dorsal view.

Fig. 296. Left maxilla, external view.

Fig. 297. Labium with left labial palpus, lateral view.

Fig. 298. Labrum, external view.

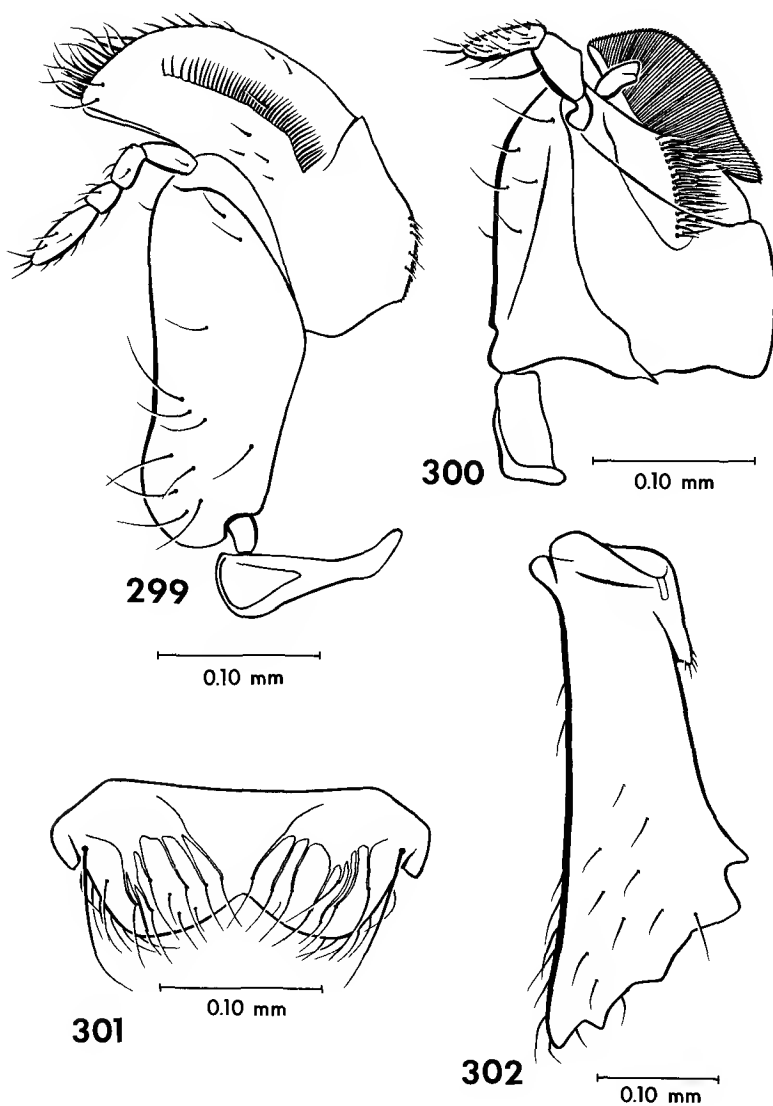


Plate 77. *Cyphomyrmex rimosus* complex (worker).

Fig. 299. Left maxilla, external view.

Fig. 300. Labium with left labial palpus, lateral view.

Fig. 301. Labrum, external view.

Fig. 302. Right mandible, dorsal view.

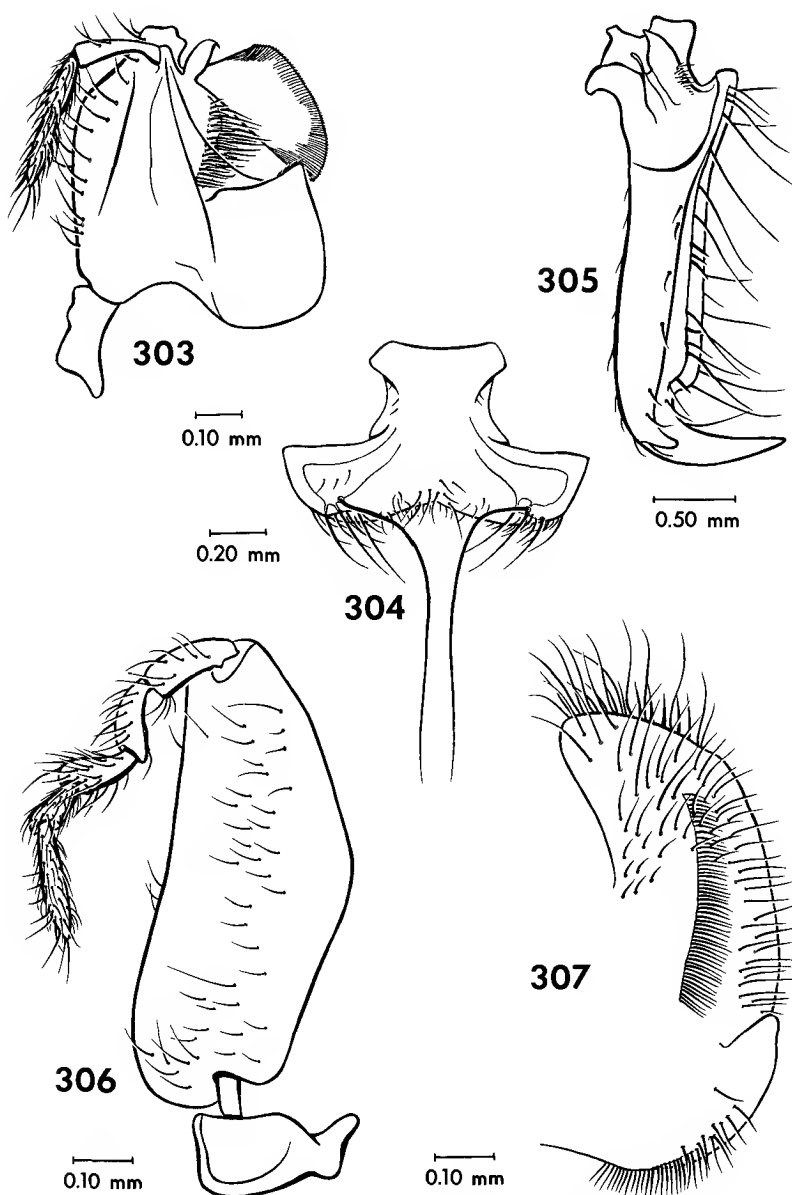


Plate 78. *Daceton armigerum* (worker).

- Fig. 303. Labium with left labial palpus, lateral view.
 Fig. 304. Labrum, external view.
 Fig. 305. Right mandible, dorsal view.
 Fig. 306. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 307. Left galea and lacinia, external view.

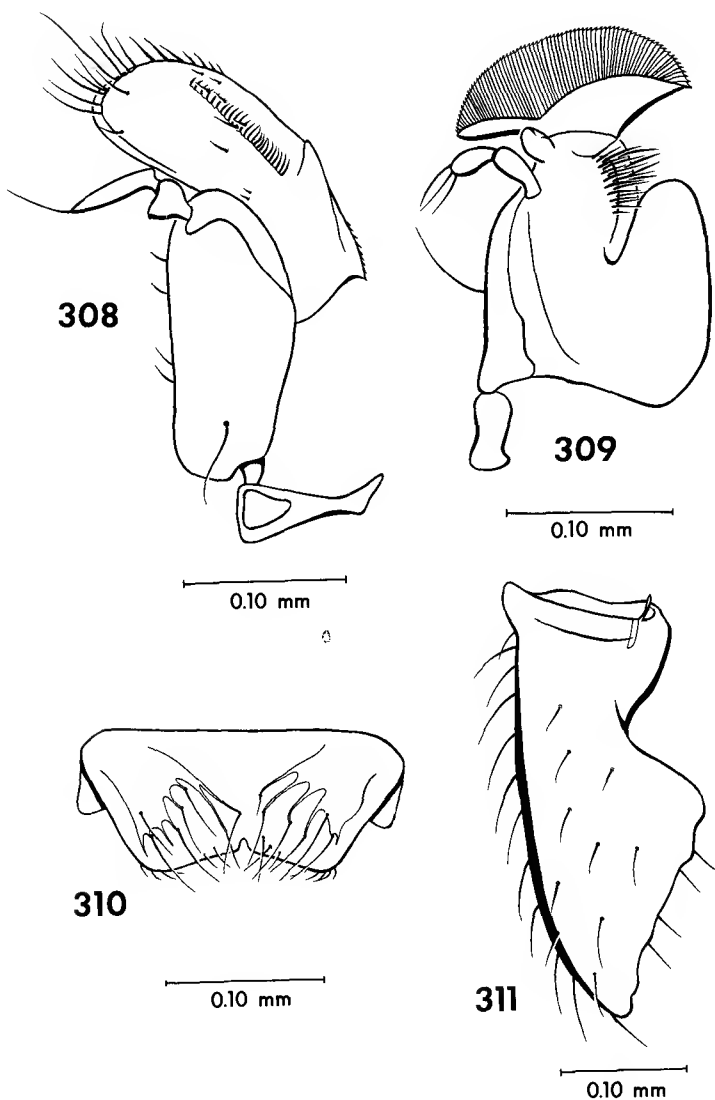


Plate 79. *Lachnomymex scrobiculatus* (worker).

Fig. 308. Left maxilla, external view.

Fig. 309. Labium, left labial palpus, lateral view.

Fig. 310. Labrum, external view.

Fig. 311. Right mandible, dorsal view.

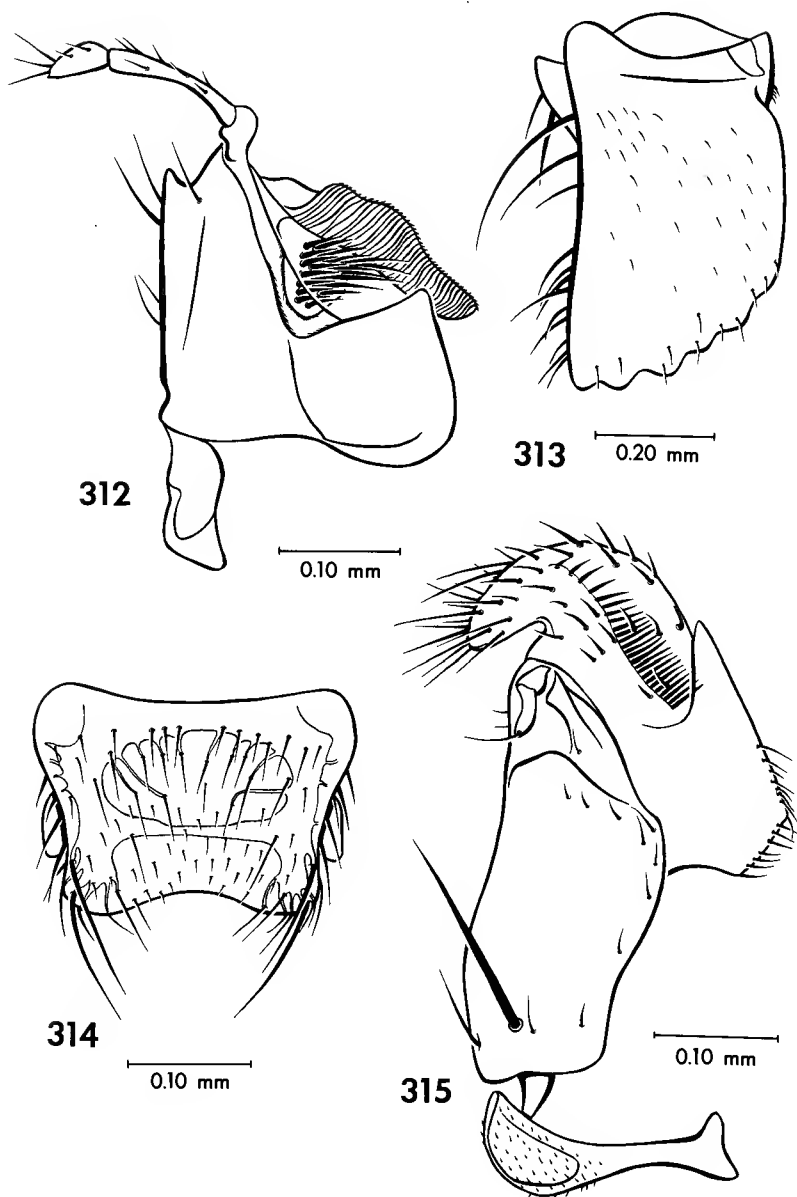


Plate 80. *Metapone truki* (worker).

Fig. 312. Labium with left labial palpus, lateral view.

Fig. 313. Right mandible, dorsal view.

Fig. 314. Labrum, external view.

Fig. 315. Left maxilla, external view.

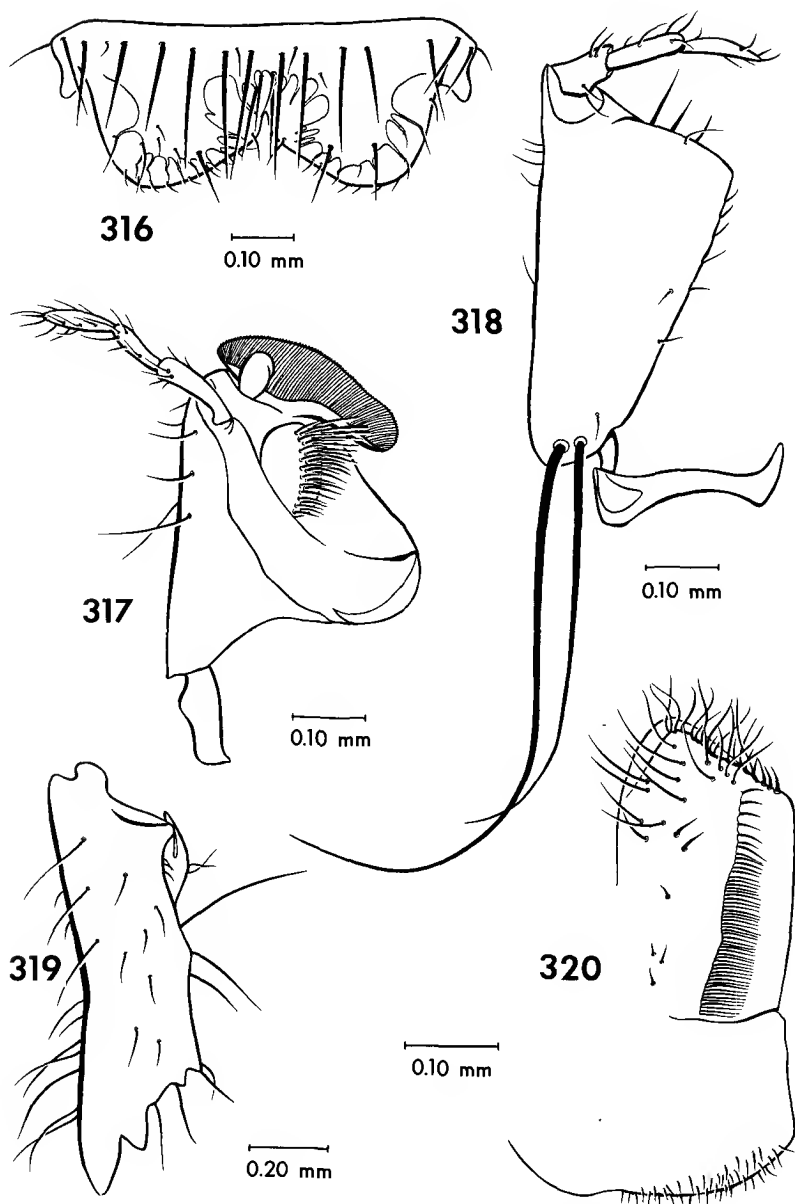


Plate 81. *Ocymyrmex barbiger* (worker).

Fig. 316. Labrum, external view.

Fig. 317. Labium with left labial palpus, lateral view.

Fig. 318. Left stipes, maxillary palpus, and cardo, external view.

Fig. 319. Right mandible, dorsal view.

Fig. 320. Left galea and lacinia, external view.

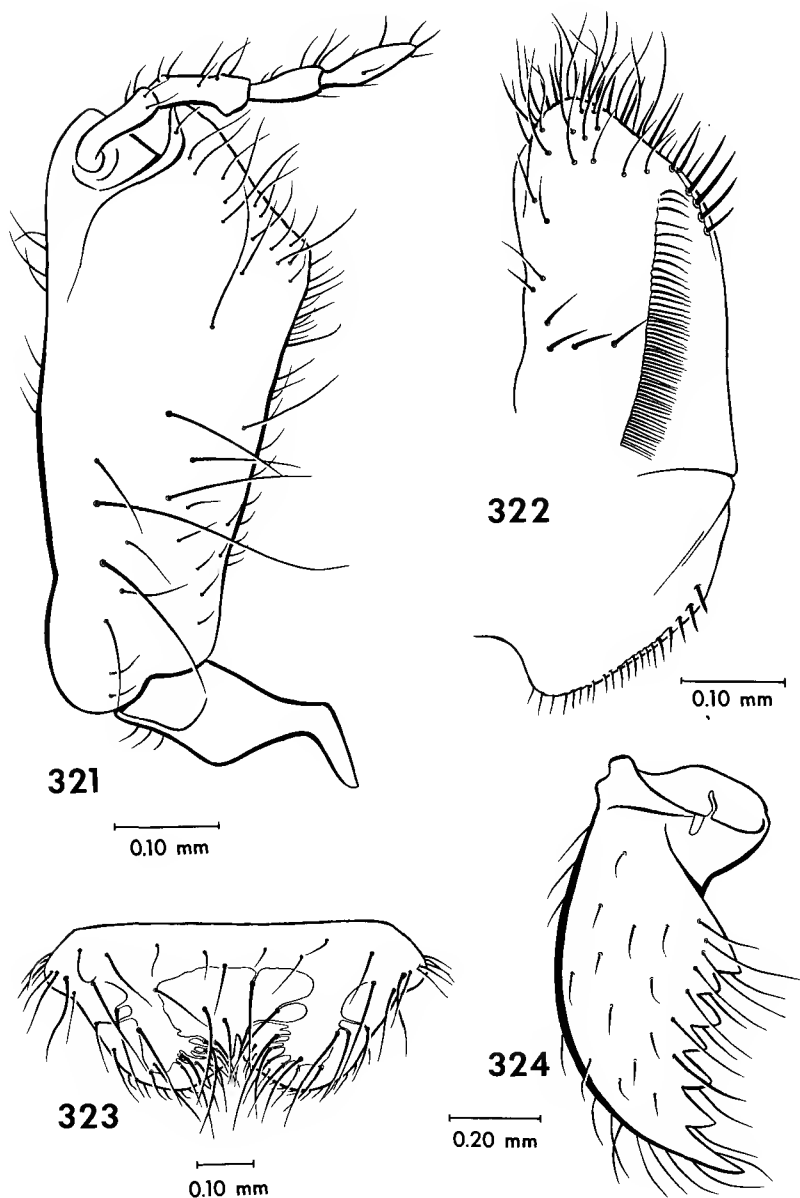


Plate 82. *Pogonomyrmex estebanius* (worker).

- Fig. 321. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 322. Left galea and lacinia, external view.
 Fig. 323. Labrum, external view.
 Fig. 324. Right mandible, dorsal view.

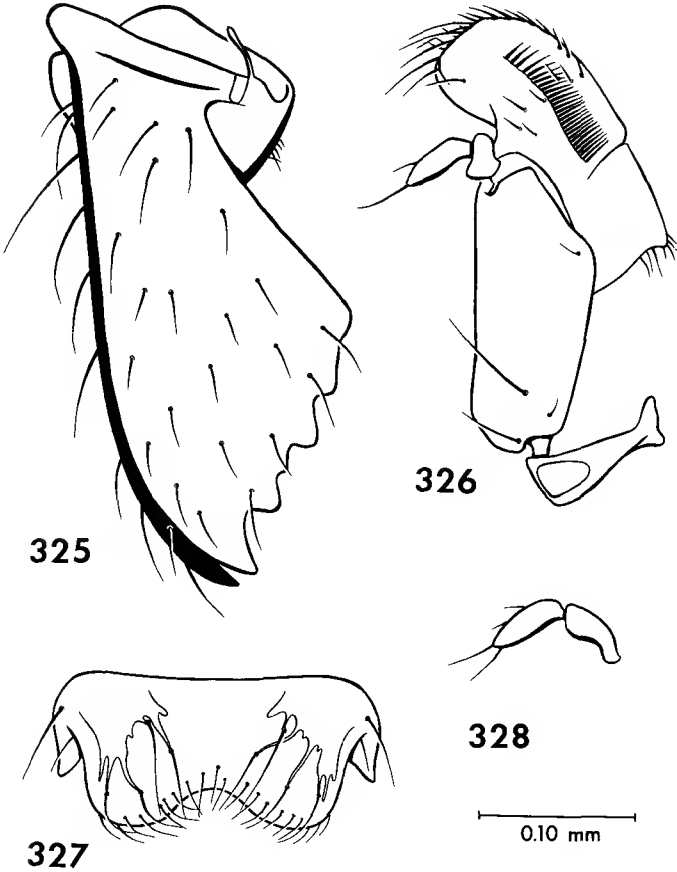


Plate 83. *Vollenhovia* n.sp. (worker).

- Fig. 325. Right mandible, dorsal view.
- Fig. 326. Left maxilla, external view.
- Fig. 327. Labrum, external view.
- Fig. 328. Left labial palpus, lateral view.

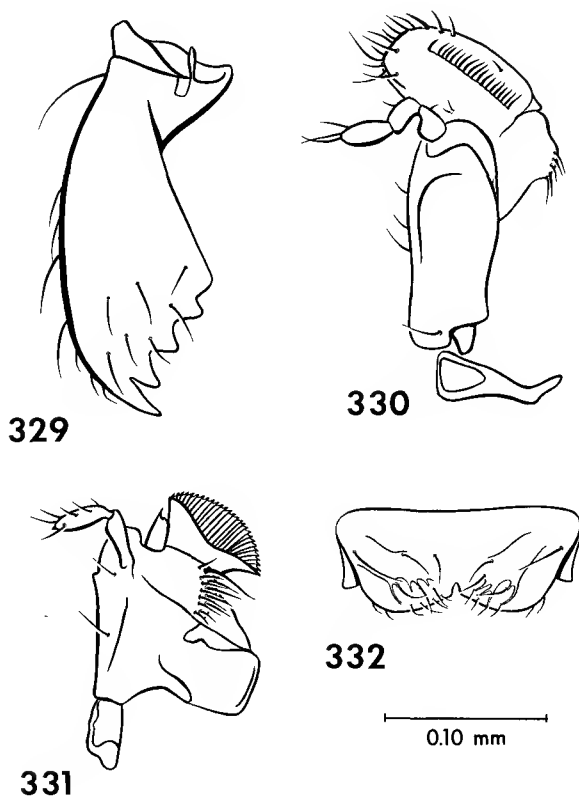


Plate 84. *Wasmannia auropunctata* (worker).

- Fig. 329. Right mandible, dorsal view.
Fig. 330. Left maxilla, external view.
Fig. 331. Labium with left labial palpus, lateral view.
Fig. 332. Labrum, external view.

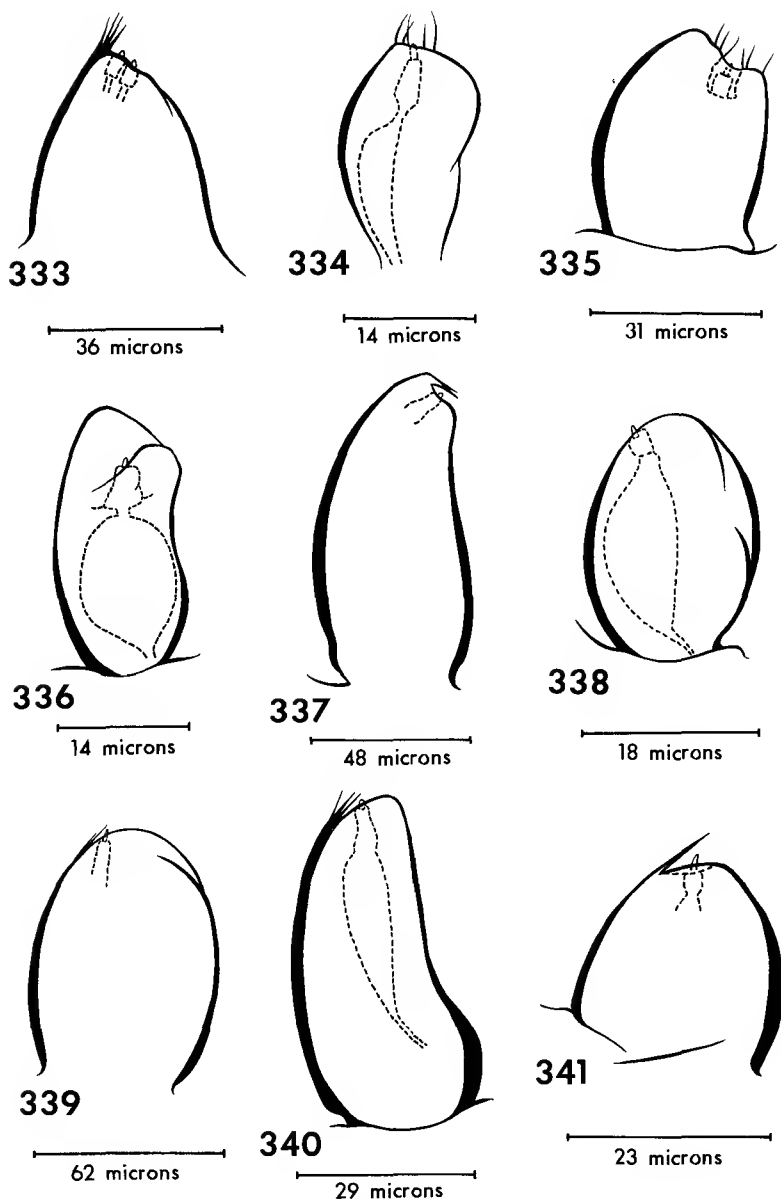


Plate 85. Left paraglossae, lateral view.

Fig. 333. *Odontomachus rixosus*Fig. 334. *Adelomyrmex tristani*Fig. 335. *Apterostigma gibbum*Fig. 336. *Cyphomyrmex rimosus* complexFig. 337. *Daceton armigerum*Fig. 338. *Lachnomyrmex scrobiculatus*Fig. 339. *Ocymyrmex barbiger*Fig. 340. *Pogonomyrmex estebaninus*Fig. 341. *Vollenhovia* n.sp.

Subfamily Myrmeciinae

Species examined:

Myrmecia auriventris (Plates 86, 87)

Labrum. The labrum is cleft or at least deeply emarginate at the middle of its distal margin, so that it is bilobed (fig. 344). The hemocoel occupies a large portion of the labrum but is absent from a circular area in each lobe. Several long setae are inserted near the distal margin. Labral tubercles are absent.

Mandible. The mandible is long and linear with 1 apical and several subapical teeth (fig. 343). Setae are not abundant and the trulleum and mandalus are present.

Maxilla. The maxillary palpus is 6-segmented. The stipes is wider distally than proximally, although the lateral shoulder is not conspicuously developed (fig. 342). Numerous setae are inserted on the external surface of the stipes. The galea is long and has a flattened galeal crown (fig. 345). A galeal comb is present, but the setae are not highly ordered. The galeal crown bears a comb of stout setae. The lacinia is subtriangulate, with a continuous lacinial comb, although the setae are somewhat scattered along the lacinial margin (fig. 345). The lacinial gonion is devoid of setae.

Labium. The labial palpus is 4-segmented (fig. 346). The premental shield is heavily sclerotized, but the epimental sclerites are not clearly defined. The subglossal brushes are composed of many long setae which taper only near their apex. Neither paraglossae nor paraglossal pegs are present, although there is a membranous structure near the usual paraglossal site.

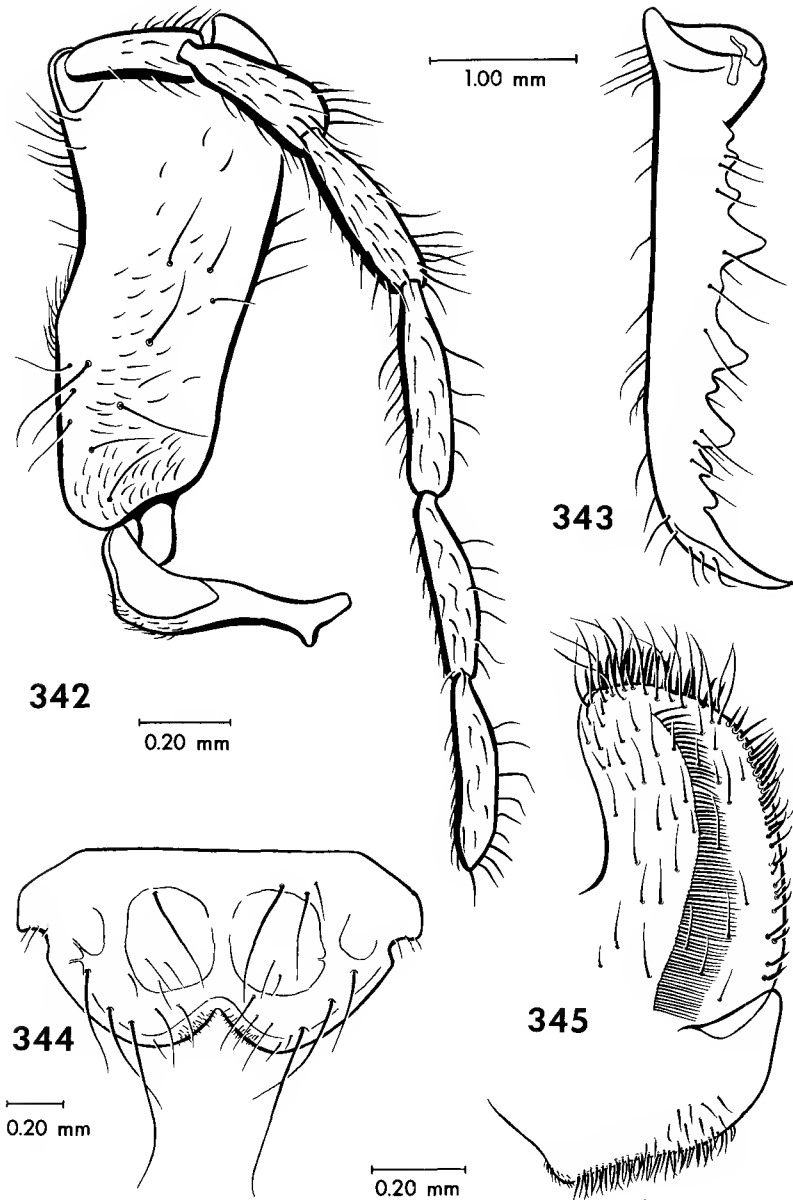


Plate 86. *Myrmecia auriventris* (worker).

- Fig. 342. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 343. Right mandible, dorsal view.
 Fig. 344. Labrum, external view.
 Fig. 345. Left galea and lacinia, external view.

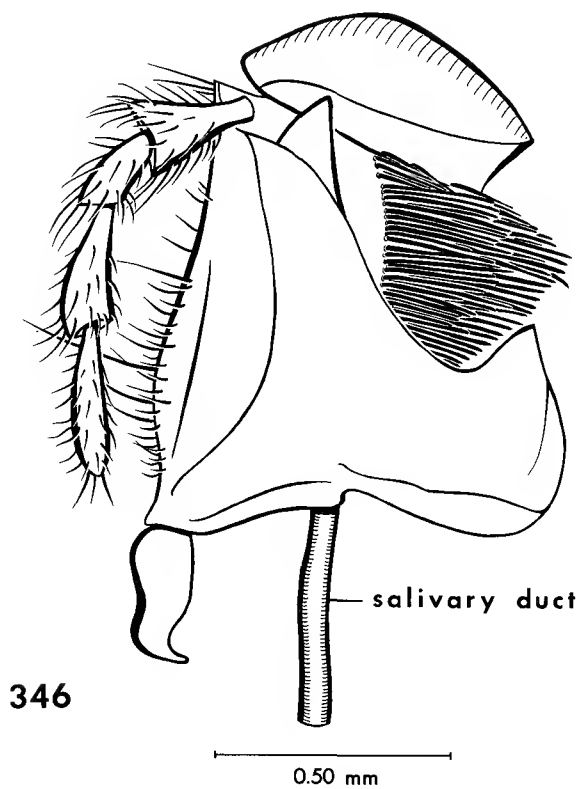


Plate 87. *Myrmecia auriventris* (worker).

Fig. 346. Labium with left labial palpus, lateral view.

Subfamily Pseudomyrmecinae

Species examined:

Pseudomyrmex gracilis group (Brazil) (Plate 88)

Pseudomyrmex sp. (Peru)

Labrum. The labrum is cleft or at least deeply emarginate at the middle of its distal margin, and bilobed (fig. 347). The hemocoel occupies almost the entire labrum. Labral tubercles are absent. In the 2 species examined the labra are indistinguishable from one another.

Mandible. The mandible is subtriangular with distinct basal and masticatory margins (fig. 348). The mandible in both species examined possesses a large apical and a subapical tooth, and *Pseudomyrmex* sp. (Peru) has, in addition, 2 small subapical teeth. In each case the basal margin has at least 1 toothlike swelling along its length. The trulleum and mandalus are present.

Maxilla. The maxillary palpus is 6-segmented. The stipes is narrow and subrectangular, and the lateral shoulder bears numerous stout setae (fig. 351). The proximal half of the stipes has a transverse groove which extends diagonally toward the lateral shoulder. It probably accommodates the distal margin of the labrum and is most strongly developed in *Pseudomyrmex* sp. (Brazil) (fig. 351). On the external surface near the proximal margin of the stipes is an exceptionally long seta. The galeal crown is flattened and has several setae, 1 or 2 of which are short and stout (fig. 350). A row of setae approximating a galeal comb is present in each species but is most highly ordered in *Pseudomyrmex* sp. (Peru). These setae are short and thin. A lacinial comb is present in addition to a series of setae irregularly placed along the lacinial margin (fig. 350). The lacinial gonion is without setae.

Labium. The labial palpus is 4-segmented. The premental shield is moderately to heavily sclerotized, while the epimental sclerites are poorly defined (fig. 349). A membranous area which seems to correspond to the raquettes is present. The subglossal brushes are composed of numerous setae, several of which are expanded and blunted apically. Paraglossae and paraglossal sensory pegs are absent.

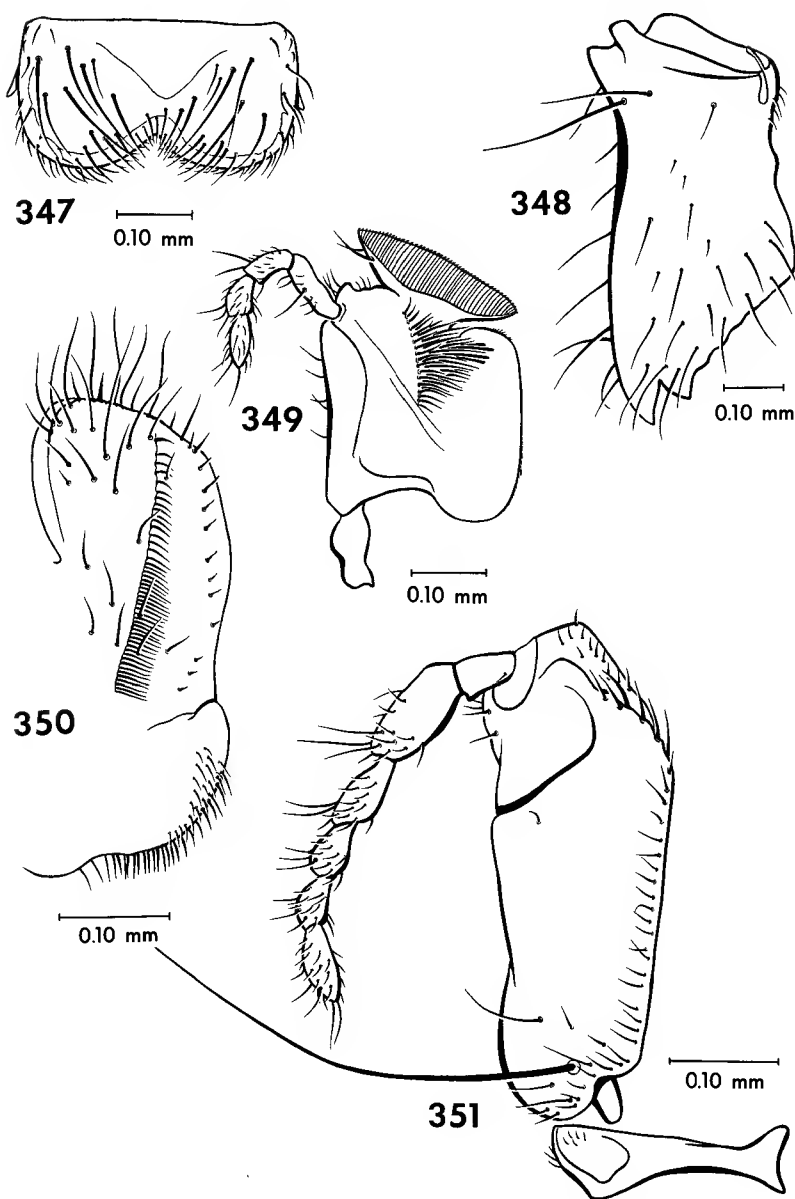


Plate 88. *Pseudomyrmex gracilis* group (worker).

- Fig. 347. Labrum, external view.
 Fig. 348. Right mandible, dorsal view.
 Fig. 349. Labium with left labial palpus, lateral view.
 Fig. 350. Left galea and lacinia, external view.
 Fig. 351. Left stipes, maxillary palpus, and cardo, external view.

Subfamily Dolichoderinae

Species examined:

Dolichoderus attelaboides (Plate 89)

Forelius foetidus

Tapinoma sessile

Labrum. The labrum is cleft in *Dolichoderus attelaboides* (fig. 355) and *Tapinoma sessile* and emarginate in *Forelius foetidus*. The labrum varies widely in shape in the species examined. The labrum of *D. attelaboides* is rectangular and prominent, while that of *F. foetidus* is reduced to such an extent that it is almost undetectable. This latter labrum forms a narrow lip below the anterior margin of the clypeus, and bears several stout setae along its distal margin. Although the labrum of *T. sessile* is also reduced, it is quite prominent, since it is heavily pigmented along the distal margin. Several stout setae are inserted along the distal margin, giving it a distinctive appearance. The hemocoel consists of 2 arms united medially in *D. attelaboides*, of 2 unconnected arms in *T. sessile*, and is of an unknown nature in *F. foetidus*. Labral tubercles are not present.

Mandible. The mandible is triangular with distinct masticatory and basal margins, and in *T. sessile* the mandible is quite broad. There was an apical tooth in all mandibles examined and numerous subapical teeth or denticles. The basal margin in *D. attelaboides* is also provided with a series of denticles (fig. 353). The trulleum and mandalus are present.

Maxilla. The maxillary palpus is 6-segmented. The stipes in the 3 species examined are all similar in shape, and *D. attelaboides* (fig. 352) is typical of this shape, except that it is proportionately wider. The lateral shoulder is evident but smoothly curved and may have numerous short setae. The galea is relatively constant in shape and the lacinia less constant. The galeal comb is flattened and bears numerous thin, long setae in addition to a row of stout setae. *D. attelaboides* (fig. 354) and *T. sessile* both have a row of short thin setae on the galea, which approximate a galeal comb. The lacinial comb is inconspicuous but continuous (fig. 354).

Labium. The labial palpus is 4-segmented. The premental shield is moderately sclerotized and the epimental sclerites poorly defined. Raquettes are absent. The subglossal brushes are composed of numerous setae, many of which are expanded and blunted apically. Paraglossae and paraglossal sensory pegs are absent.

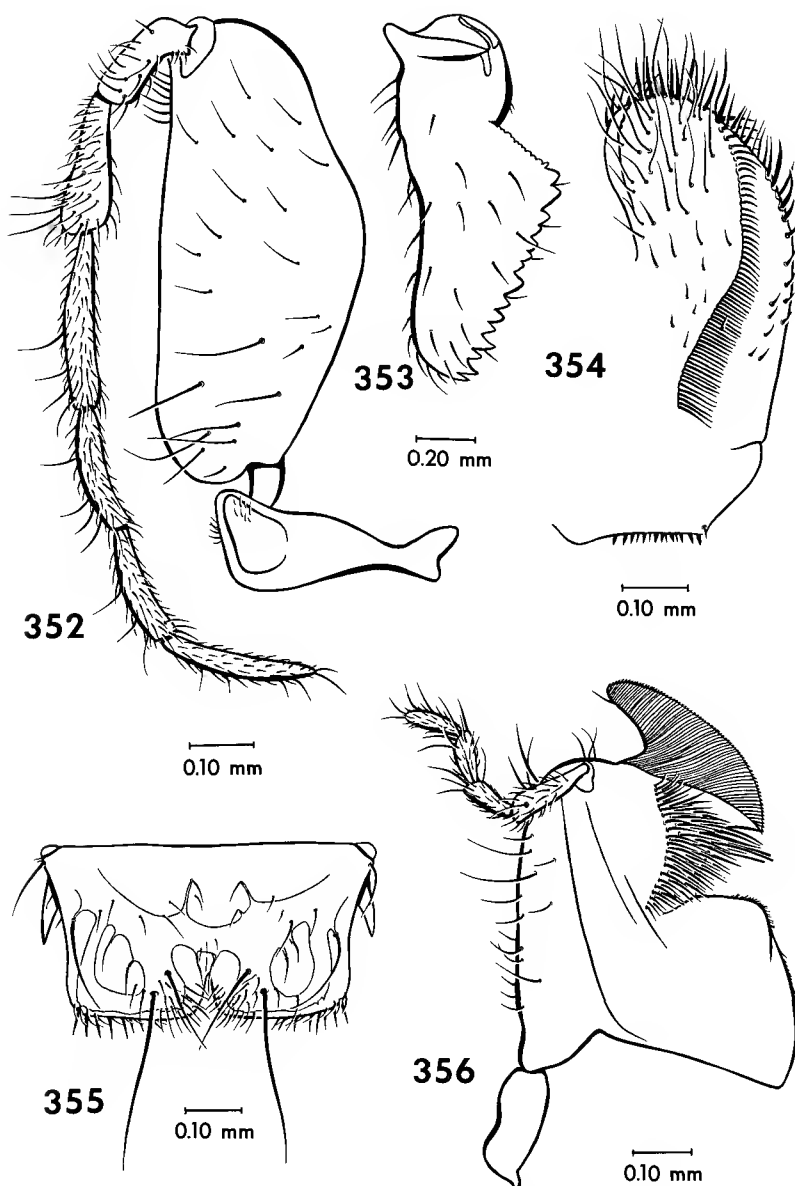


Plate 89. *Dolichoderus attelaboides* (worker).

- Fig. 352. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 353. Right mandible, dorsal view.
 Fig. 354. Left galea and lacinia, external view.
 Fig. 355. Labrum, external view.
 Fig. 356. Labium with left labial palpus, lateral view.

Subfamily Formicinae

Species examined:

Acropyga sp. (Plate 90)

Camponotus noveboracensis
(Plate 91)

Formica exsectoides

Gigantiops destructor (Plate 92)

Myrmelachista paderewskii

Prenolepis imparis (Plate 93)

Prolasius nitidissimus

Labrum. The labrum is cleft or emarginate medially, or both. It is most deeply emarginate and cleft in *C. noveboracensis* (fig. 361) and most weakly emarginate in *Acropyga* sp. (fig. 357). Generally the labrum is rectangular or subquadrate with distinct distal and lateral margins. The lateral margins are often slightly emarginate as in *C. noveboracensis* (fig. 361) and *G. destructor* (fig. 369). In *Acropyga* sp. (fig. 357) and *P. imparis* (fig. 372), the proximal lateral angles of the labrum are highly modified. The hemocoel consists of 2 arms, one in each lobe, which may almost fill the entire labrum as in *G. destructor* (fig. 369). The distribution of setae departs most radically from the general pattern for the group in *Acropyga* sp. (fig. 357), with the largest concentration of heavy setae along the distal lateral angles. Labral tubercles are absent in the formicines.

Mandible. The mandibles are usually broad and triangular. The mandible is most narrowly developed in *Acropyga* sp. (fig. 360) and most broadly developed in *C. noveboracensis* (fig. 363). The masticatory and basal margins are clearly defined, and the masticatory margin is provided with prominent teeth. The number of subapical teeth is usually 4 or more, although there are only 2 in *Acropyga* sp. (fig. 360). The trulleum and mandalus are distinct in all the species except *Acropyga* sp.

Maxilla. The maxillary palpus is 6-segmented in all species examined except *Acropyga* sp. (fig. 359) in which it is 1-segmented. The shape of the stipites is not uniform and 4 "types" were delineated. The shape of the stipes of *Acropyga* sp. (fig. 359), although similar to that of *P. imparis*, is provided with numerous long setae and a single-segmented palpus. The stipites of *Prenolepis* (fig. 371) and *Prolasius* are of the same shape, each having a distinct but rounded lateral shoulder with several short setae. *Camponotus* (fig. 365), *Gigantiops* (fig. 366), and *Formica* all share a similarly shaped stipes, which is narrowed distally and almost pointed at the insertion of the palpus. In these species the lateral shoulder has short

setae. While the stipes of *Myrmelachista paderewskii* is proportionately wider than that of *Camponotus noveboracensis* and has a more clearly defined lateral shoulder, it probably should be placed with the *Camponotus* type. The galea is most commonly shaped like that of *C. noveboracensis* (fig. 364) or *P. imparis* (fig. 371), and has a flattened galeal crown. In *C. noveboracensis* and *P. imparis* there are rows of setae resembling, in terms of their position, galeal combs. In addition to numerous long, thin setae on the crown, there is usually a series of short, stout setae. The lacinia is subtriangular with a rounded or poorly defined apex. The lacinial comb is conspicuous only in *C. noveboracensis* (fig. 364), but it is present and continuous in all species examined.

Labium. The labial palpus is 4-segmented in all species except in *Acropyga* sp. in which it is 3-segmented. The premental shield varies widely in degree of sclerotization, and the epimental sclerites are quite evident although not always clearly defined distally. Raquettes are not present, although *P. imparis* (fig. 374) does possess raquette-like membranous expansions. The subglossal brushes are usually composed of many setae, as in *C. noveboracensis* (fig. 362), which taper throughout their length and are pointed apically. Paired paraglossae without sensory pegs are present in *Acropyga* (fig. 358) and absent in all other species.

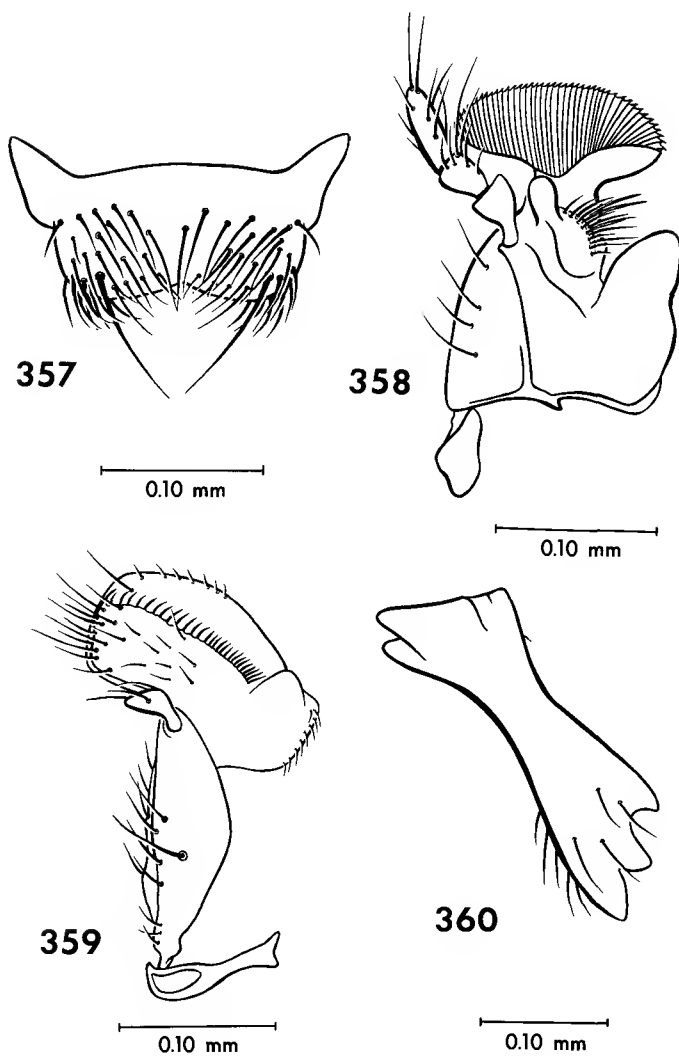


Plate 90. *Acropyga* sp. (worker).

- Fig. 357. Labrum, external view.
Fig. 358. Labium with left labial palpus, lateral view.
Fig. 359. Left maxilla, external view.
Fig. 360. Right mandible, dorsal aspect.

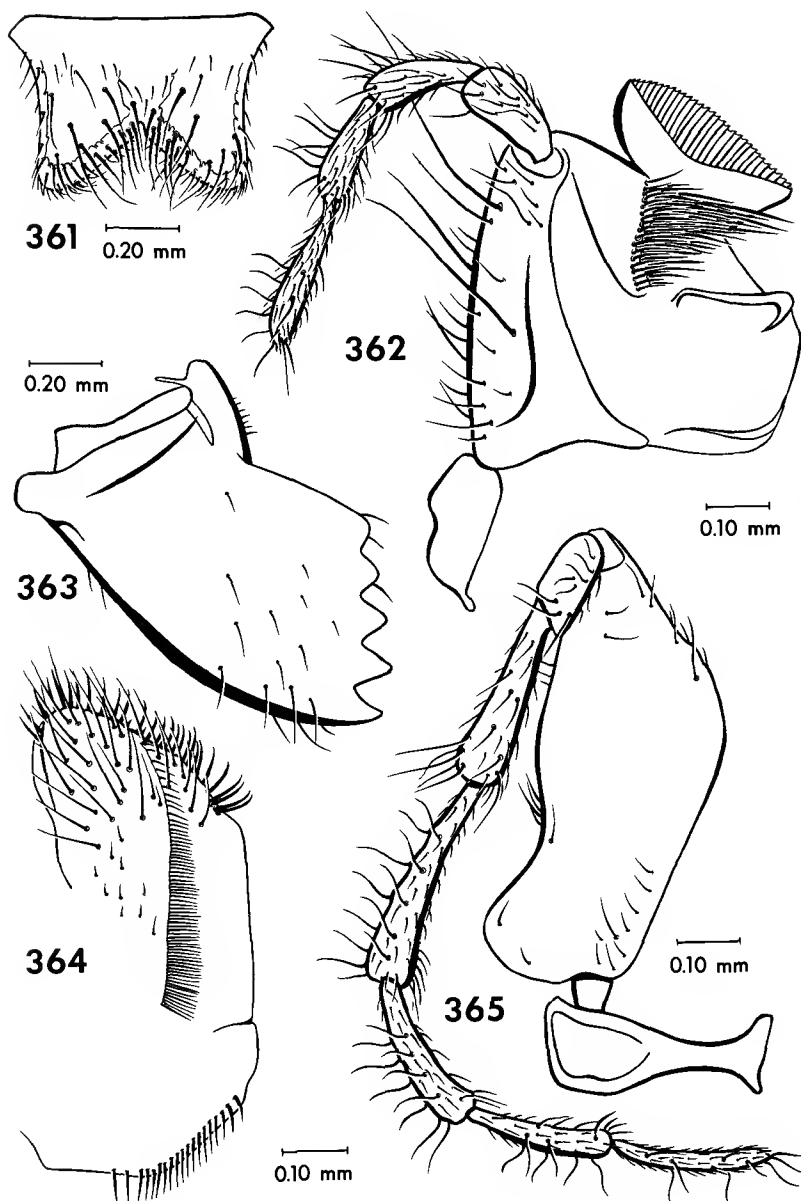


Plate 91. *Camponotus noveboracensis* (worker).

- Fig. 361. Labrum, external view.
 Fig. 362. Labium with left labial palpus, lateral view.
 Fig. 363. Right mandible, dorsal view.
 Fig. 364. Left galea and lacinia, external view.
 Fig. 365. Left stipes, maxillary palpus, and cardo, external view.

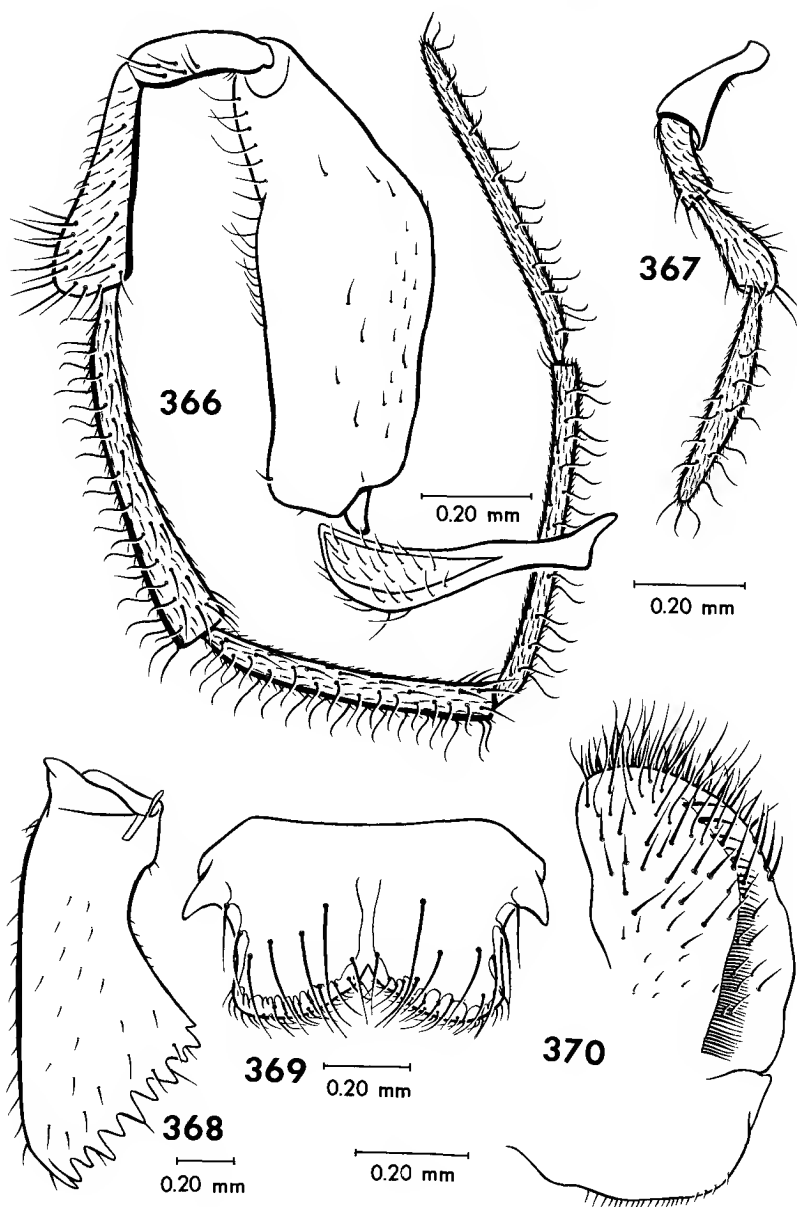


Plate 92. *Gigantiops destructor* (worker).

- Fig. 366. Left stipes, maxillary palpus, and cardo, external view.
 Fig. 367. Left labial palpus, lateral view.
 Fig. 368. Right mandible, dorsal view.
 Fig. 369. Labrum, external view.
 Fig. 370. Left galea and lacinia, external view.

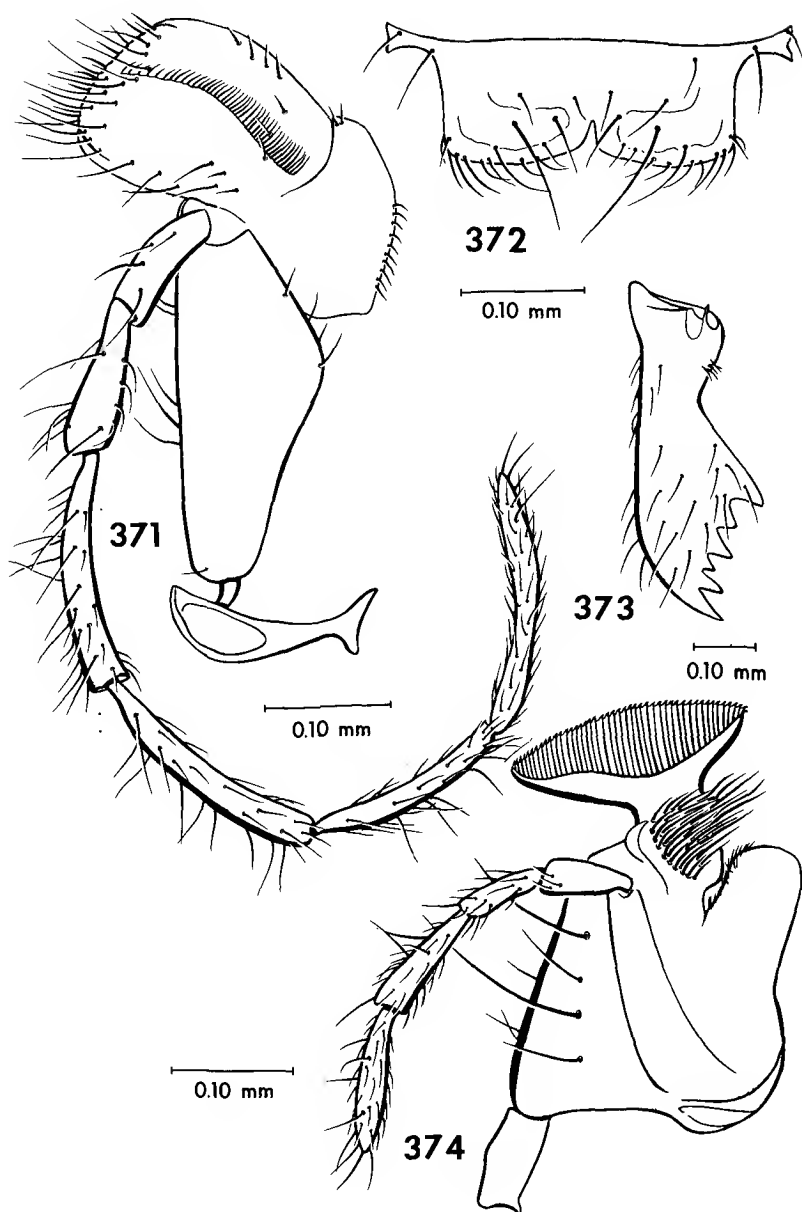


Plate 93. *Prenolepis imparis* (worker).

Fig. 371. Left maxilla, external view.

Fig. 372. Labrum, external view.

Fig. 373. Right mandible, dorsal view.

Fig. 374. Labium with left labial palpus, lateral view.

Condition of Gastral Sclerites in Representative Species

The sclerites examined are those of the first and second segments of the gaster. If the pedicel is 1-segmented, these gastral segments constitute the third and fourth abdominal segments, and if the pedicel is 2-segmented, they constitute the fourth and fifth abdominal segments. For each of these 2 segments, the condition of the sclerites with respect to the fusion of the tergite of 1 segment to the sternite of the same segment was determined. Particular attention was given to the subfamilies Ponerinae, Cerapachyinae, Dorylinae, and Myrmicinae, since it is within these groups that this condition of fusion is of greatest phylogenetic importance. Only workers were examined except where otherwise indicated.

Subfamily Ponerinae

Species examined:

<i>Ectatomma tuberculatum</i>	<i>Pachycondyla crassinoda</i>
<i>Gnamptogenys schubarti</i>	<i>Paraponera clavata</i>
<i>Hypoponera opacior</i>	<i>Platythyrea schultzei</i>
<i>Leptogenys</i> cf. <i>crassicornis</i>	<i>Rhytidoponera turneri</i>
<i>Megaponera foetens</i>	<i>Simopelta oculata</i>
<i>Myopias</i> n. sp. in <i>maligna</i> group	<i>Termitopone commutata</i>
<i>Odontomachus rixosus</i>	<i>Typhlomyrmex rogenhoferi</i>

The tergites are fused to the sternites in both segments in all species examined except *Gnamptogenys schubarti* and *Rhytidoponera turneri*, in which the first gastral segment (third abdominal) seemed to be unfused and the second fused. In these 2 species the condition of the first gastral segment was difficult to determine. Although the tergites and sternites of this segment are tightly joined, they separate cleanly when strongly pulled.

Subfamily Cerapachyinae

Species examined:

<i>Acanthostichus</i> sp. near <i>quadratus</i>	<i>Cylindromyrmex striatus</i>
<i>Cerapachys opaca</i>	<i>Sphinctomyrmex steinheili</i>
<i>Cerapachys</i> sp.	

In all species examined, the sclerites of the first gastral segment (third abdominal) are fused and those of the second segment unfused. However, in *Cerapachys* sp. and *Sphinctomyrmex steinheili*, the sclerites of the second gastral segment are tightly held together.

Subfamily Dorylinae

Species examined:

<i>Aenictus aratus</i>	<i>E. hamatum</i>
<i>A. gracilis</i>	<i>E. lucanoides</i>
<i>A. laeviceps</i>	<i>E. mexicanum</i>
<i>A. ceylonicus</i>	<i>E. quadriglume</i>
<i>A. sp. (male)</i>	<i>E. rapax</i>
<i>Cheliomyrmex morosus</i>	<i>Labidus coecus</i>
(worker, male)	<i>L. praedator</i>
<i>Dorylus (Alaopone) orientalis</i>	<i>Neivamyrmex carolinensis</i>
<i>D. (Anomma) emeryi</i>	<i>N. harrisi (male)</i>
<i>D. (Dichthadia) laevigatus</i>	<i>N. laevigatus</i>
<i>D. (Dorylus) helvolus</i>	<i>N. nigrescens</i>
<i>D. (Typhlopone) fulvus (male)</i>	<i>N. opacithorax</i>
<i>D. (Typhlopone) labiatus</i>	<i>N. pilosus</i>
<i>D. (Typhlopone) dentifrons</i>	<i>N. sumichrasti</i>
<i>Eciton burchelli</i> (worker, male)	<i>N. swainsoni (male)</i>
<i>E. drepanophorum</i>	<i>N. wheeleri</i>
<i>E. dulcius</i>	<i>Nomamyrmex esenbecki</i>

In the workers of the genus *Aenictus*, the sclerites of the first and second gastral segments (fourth and fifth abdominal) are unfused. In the male, however, where the first and second gastral segments are the third and fourth abdominal segments, the tergite and sternite of the first gastral are fused. Throughout the genus *Dorylus*, in both workers and males, the first gastral segment (third abdominal) is fused, and the second is unfused. The first gastral segment (third abdominal) of *Cheliomyrmex morosus* workers and males is fused and the second is unfused. In the male of this species, however, the fusion of the tergite and sternite of the first gastral segment is not complete posteriorly. In the workers of all genera of Ecitonini both gastral segments (fourth and fifth abdominal) are fused. The first gastral segment (third abdominal) of the male of *E. burchelli* is fused and the second unfused; however, in the males of *Neivamyrmex harrisi* and *swainsoni*, the third abdominal segment remains unfused.

Subfamily Myrmicinae

Species examined:

<i>Adelomyrmex tristani</i>	<i>Lachnomyrmex scrobiculatus</i>
<i>Aphaenogaster rudis</i>	<i>Melissotarsus beccarii (queen)</i>
<i>Apterostigma gibbum</i>	<i>Meranoplus dichrous</i>
<i>Blepharidatta brasiliensis</i>	<i>Messor barbarus</i>
<i>Crematogaster cf. brasiliensis</i>	<i>Metapone truki</i>
<i>Cyphomyrmex rimosus complex</i>	<i>Ocymyrmex barbiger</i>
<i>Daceton armigerum</i>	<i>Pheidole desertorum</i>

*Pogonomyrmex estebanius**Vollenhovia* n. sp.*Solenopsis texana**Wasmannia auropunctata**Tetramorium pacificum*

Both gastral segments (fourth and fifth abdominal) are unfused in the workers of myrmicine ants. This is true also for the queen of *Melissotarsus beccarii* examined.

Subfamily Myrmeciinae

Species examined:

Myrmecia auriventris

The first and second gastral segments (fourth and fifth abdominal) of *M. auriventris* are unfused.

Subfamily Pseudomyrmecinae

Species examined:

Pseudomyrmex gracilis group (Brazil)*Pseudomyrmex* sp. (Peru)

Both gastral segments (fourth and fifth abdominal) of the workers of the pseudomyrmecine species examined are unfused.

Subfamily Dolichoderinae

Species examined:

Dolichoderus attelaboides

Both gastral segments (third and fourth abdominal) are unfused.

Subfamily Formicinae

Species examined:

Acropyga sp.*Myrmelachista paderewskii**Camponotus noveboracensis**Prenolepis imparis**Formica exsectoides*

The first and second gastral segments (third and fourth abdominal) of the workers examined are unfused.

Discussion

Mouthpart Morphology and Function

An attempt was made throughout this investigation to distinguish between the cleft and emarginate conditions of the distal margin of the labrum. A cleft was defined as being usually narrow and slitlike, although its width did vary to such a degree that certain labra could not be distinguished as being strictly cleft or emarginate. The utility of such a distinction, either in viewing phylogeny or just in identifying specimens, is questionable. It is clear, however, that in some specimens there are distinct differences in the condition of the distal margin. The difference between *Cylindromyrmex striatus* (slightly emarginate) and the remaining cerapachyines (distinctly cleft) or between the Dorylini (neither emarginate nor cleft but smoothly rounded) and the Ecitonini (distinctly cleft) are of this magnitude and cannot be ignored. The labrum seems to be of potential taxonomic importance, and this potential has been little realized. The shape of the labrum is more or less a reflection of the condition of the distal margin, although it is also affected by the ratio of its width to its length and occasionally by the unusual development of the proximal lateral angles [e.g. in *Prenolepis imparis* (fig. 372)]. The labral tubercles which appear in the workers of the Dorylini, Ecitonini, and the genus *Acanthostichus* are of unknown function, although, since the males and queens of the dorylines do not possess such structures, it is assumed that their function is related to worker activities such as foraging (e.g., helping to hold active prey). To further complicate this situation, there may be at least 2 types of tubercles, one that is distinctly a lamina-like projection of the cuticle and another whose nature is not clear. This latter type does break from the labral surface easily and is usually peglike and blunted apically. Labral tubercles may function with the labrum in manipulating food materials or in a sensory capacity. This investigation indicated that the tubercles may be restricted to a relatively small group of species. Since setal patterns on the labrum have not been discussed in detail in the descriptions, the drawings should be consulted. What should be determined, for perhaps 1 or 2 species, is the constancy of setal placement, at least for the larger setae. Because this has not been done, it is difficult to comment comparatively on setal patterns. In some species [e.g. *Acropyga* sp. (fig. 357)], setal distribution departs radically from what is commonly found in other species. In general, the labrum is usually provided with several long setae that seem to be consistently placed within certain species groups. The distal margin always has numerous small setae. The hemocoel enters the labrum proximally as a wide cavity, and then commonly divides into 2 arms, which may or may not unite again behind the middle of the distal margin. In some castes (e.g., males and queens of Ecitonini), the hemocoel does not divide, and seems to fill the entire labrum except for a narrow band along the distal margin. The constancy of the hemocoel in terms of

shape has not been studied in detail for any one species. In fact, the shape of the hemocoel and the distribution of the setae are strongly related in that each seta is narrowly connected with the hemocoel.

Of the mouthparts, the mandibles have been most commonly used by taxonomists in the classification of ants. Although mandibular shape and dentition can be indicators of phylogenetic trends within species groups (Brown and Wilson, 1959; Ettershank, 1966; and Wilson, 1955), it is difficult to see such trends in the family Formicidae as a whole. The ant mandible is commonly broad and triangular with a distinct masticatory and basal margin. In the males and females of the dorylines, the mandibles always depart from this pattern, and modifications occur also among some soldiers (e.g. *Eciton*, *Dorylus*). While the mandibles of such soldiers are superficially quite distinct from those of other workers, they may, in fact, be part of a continuous series with respect to shape. Hollingsworth (1960), in refuting Cohic's (1948) contention that the workers of *Dorylus* (*Anomma*) *nigricans* exist in 4 distinct morphological types, was able to arrange the worker mandibles of this species in a completely continuous series. It appears that in *Cheliomyrmex morosus* such a continuous series could also be arranged, but this is less probable for *Eciton*. While the morphological condition of the mandible of workers is probably an adaptation to foraging behavior and perhaps brood care, that of the males may be an adaptation to copulatory behavior. Schneirla (1949) and Rettenmeyer (1963) have both reported matings of *Eciton* species (*hamatum* and *burchelli* respectively), in which the male uses its mandibles to grasp the queen's petiole. Rettenmeyer (1963) suggested that the male's behavior may indicate that contact between the male mandibles and the queen petiole is an important stimulus in mating and perhaps that such contact is even important in preventing interspecies mating. The mandalus is common to all species and castes, although it is sometimes difficult to detect in darkly pigmented mandibles. Ettershank (1966) suggested that the mandalus may contain the orifice of the duct from the mandibular gland, but this was neither confirmed nor disproved in this investigation. The trulleum, a groove or depression that sometimes accommodates a portion of the distal margin of the head, is usually present, but may be absent in falcate mandibles of males and queens. While Ettershank (1966) found the condition of the trulleum quite useful taxonomically among certain myrmicines, it apparently does not vary greatly among the ants as a family. The abundance and pattern of distribution of mandibular setae varies widely, but in general the dorsal surface of the mandible has fewer setae than the ventral surface. On the ventral surface, these setae may form combs.

The number of segments in the maxillary palpus, as pointed out by Kusnezov (1954a, 1954b), is least modified in ants that he believed to be "socially advanced" (Dolichoderinae and Formicinae). But palpal reduction is apparently not affected by level of social development (if this can be satisfactorily defined). Instead, reduction seems to be correlated with

the mode of life, epigaeic or hypogaeic, to which a species is adapted. In species that are strongly hypogaeic, reduction in the number of palpal segments is always evident. Such reduction can be seen not only in the Ponerinae, Cerapachyinae, Dorylinae, Leptanillinae, and Myrmicinae but in the Formicinae (*Acropyga*) as well.

The lateral shoulder of the stipes is most prominently developed in the Dorylinae, particularly in the Ecitonini and the genus *Dorylus*. Where well developed, it also has stout setae. The placement of such setae is probably less related to feeding (on the basis of their position when the mouthparts are extended) than are the setae of the galea and lacinia.

The transverse stipital groove is found in several groups: in certain ponerines (*Amblyopone*, *Rhytidoponera*, *Gnamptogenys*, and *Typhlomyrmex*), throughout the Cerapachyinae, Ecitonini, and the genus *Dorylus*, and in the Pseudomyrmecinae. Its function in forming a protective shield, with the labrum, for the retracted maxillo-labial complex has been discussed. This groove seems most strongly developed among the Cerapachyinae and the Ecitonini.

The cardo varies primarily in terms of its relative length, but, for the most part is uniform throughout the ants. The cardo is broadened in the area of articulation with the stipes, and in this area the cuticle is translucent at the center and ringed by a thickened ridge on the internal surface of the structure.

The galeal crown is usually quite distinct throughout the ants and is commonly flattened. It is most prominently developed in the doryline genus *Dorylus*, forming a conical protuberance (see fig. 154). Bugnion (1930) described this protuberance for the soldier of *D. (Anomma) wilverthi* as being located in a limited depression on the ventral surface of the galea, and indicated that the ant could probably move it like an appendage. The material examined in this investigation does not indicate that the crown is situated in a depression. The maxillary comb is a universal characteristic of the ants. It is nearly always well developed, and, because of its ubiquitous nature, is not a taxonomically useful character. The variation that does occur is in the number and size of the setae in the comb. The galeal comb is most prominently developed in the Ecitonini, and the setae which make up the comb are of a peculiar shape. Other groups that have galeal combs made of these ecitonine-type setae are the cerapachyines and certain ponerines. The function of this comb has not been investigated, and although it is tempting to relate it to army ant foraging behavior, it is notably absent in such a species as *Simopelta oculata*, which has been described as army-antlike in its behavior (Gotwald and Brown, 1966). In some species such as *Rhytidoponera turneri* (fig. 80), a row of setae is in the galeal comb position and may function as do other galeal combs, but the setae are not of the ecitonine type.

Although the lacinia may occasionally be rounded and without a distinct apex, it is usually triangular throughout the ants. When the mouthparts

are extended, the laciniae partly cover the labial groove, and the lacinial comb apparently is used to pass materials along this groove. But the comb is not always present, or if so, may be small and inconspicuous. It is usually continuous, though discontinuous in some sexual forms. Conspicuous setae are sometimes present on the lacinial gonia, as in *Dorylus*.

As with the maxillary palpus, the labial palpus has fewer segments in species that are strongly hypogaecic. A distinct sensory peg is often found at or near the tip of the last labial palpus segment in the Dorylinae; this is most noticeable and constant in the genus *Aenictus* (fig. 123). The shape of the labial palpus in *Aenictus* is also quite constant. Although this palpus is reduced to 2 segments in many species, the segments are much less highly modified than they are in the genus *Dorylus*. In *Dorylus*, the palpal segments are elongated and rodlike (fig. 151).

The prementum is similar in its basic construction throughout the ants, although the premental shield may vary in degree of sclerotization or differ in shape. The premental shield always extends laterally along the labium, where it becomes membranous. The proximal lateral corners, which are extended laterally, are usually heavily sclerotized, and serve as points for muscle insertion. While heavy sclerotization of the premental shield provides greater protection for the mouthparts, and while this protection may be of greater advantage among active foragers and predators, such heavy sclerotization seems to be absent in the Dorylinae. In this connection it is important to note that, in the Dorylini and Ecitonini, the labrum and stipites together effectively cover the premental shield when the maxillo-labial apparatus is retracted. The premental shield commonly has several long setae, which extend out beneath the mandibles when the mouthparts are withdrawn and may serve as tactile sense receptors. Prominent setae, for instance, occur on the prementum of *Paraponera clavata* (figs. 66, 67) and of the male of *Dorylus fulvus* (fig. 173).

The proximal lateral extensions of the premental shield articulate with the epimental sclerites. These supporting sclerites are present in all ants but are seldom clearly defined. They are membranous in part and difficult to discern. In 1925, Bugnion indicated that these sclerites terminated distally in brown triangular expansions that he called the *raquettes*. He also described the *raquettes* as being provided with muscles whose action probably assisted the progress of particles along the labial groove. In the present investigation the *raquettes* were never clearly seen as the distinct structures described by Bugnion. In only a few species [e.g. *Eciton quadriglume* soldier (fig. 240)] were there any structures that even remotely resembled the *raquettes*, and these appear to be membranous expansions associated with the labial groove and infrabuccal pocket and not with the epimental sclerites. It is suggested, therefore, that the term *raquette* be abandoned.

In 1925 also, Bugnion indicated that the term paraglossa was not accurate in describing the subglossal brush and the plate on which it is inserted, insisting that the subglossal brushes were not, in fact, homologues of

the paraglossae of other insects. The function of these collections of setae has not been investigated, but they are probably active in both feeding and grooming. The subglossal brushes are present in all castes of all ants and are situated at the base of the glossa. One curiosity that these setae do present is their variety of shape, even within a single brush. The brushes generally point back toward the labial groove.

The glossa is always a prominent feature of the labium; it is always covered distally by a series of transverse ridges and nearly always surrounded at its base by a series of pores, called by Forel (1874) the *gustatory papillae*. The transverse ridges of the glossa seem to consist of series of scales that may possibly comprise highly modified setae. Weight is lent to this possibility by the presence on tiphiid glossae of what appear to be large numbers of setae.

For *Atta sexdens*, Bugnion (1930) described a pair of structures, inserted near the base of the glossa, which he described as cylindrical, transparent pegs (*bâtonnets*). In this investigation, such transparent structures were found in every myrmicine species examined (except *Metapone truki* and the queen of *Melissotarsus beccarii*) and, in addition, in some ponerines and one formicine (see figs. 333–341). These were called, for the lack of a better term, the paraglossae, but whether they are actually homologues of other insect paraglossae is not known. They are so transparent and delicate that they first escaped detection. They are generally situated diagonally in front of the subglossal brushes toward the labial palpi. In the myrmicines each is fitted terminally with a prominent sensory peg which may or may not be protected by a series of setae. Bugnion (1930) did not detect the sensory peg, if present in *Atta*, and suggested that these transparent structures were probably tactile sensory receptors. Present knowledge of complex ant chemosensory behavior patterns would suggest that they probably are chemoreceptors. Such structures also appear in several ponerines and are most highly developed in *Odontomachus rixosus* (fig. 333), which possesses 2 sensory pegs per paraglossa instead of 1. Sensory pegs are absent from the paraglossae of some ponerines [e.g. *Amblyopone* (fig. 29)], and in some species pegs are present without the development of the paraglossae, ranging in number from 1 to 3 on each side. A pair of paraglossae without pegs is also present in the formicine *Acropyga* sp. (fig. 358). Sensory pegs of the type found on the paraglossae sometimes occur also on the anterior tip of the glossa. These were noted by Forel (1874) and called *gustatory papillae*.

In viewing the mouthparts as a whole, one overriding factor becomes evident: the ants rely heavily on the presence and placement of setae in mouthpart function. Devising methods for testing the functions of various setal groups will be extremely difficult but well worth the effort. These setae no doubt combine to supply sensory information, both tactile and chemical, about the environment, including food materials and other ants, and perform passive mechanical operations in grooming and passing food along the labial groove toward the digestive tract.

Fusion of Gastral Sclerites

The fusion or non-fusion of the tergites to the sternites of the first 2 gastral segments depends partly on whether these first 2 segments are the third and fourth or the fourth and fifth abdominal segments. In the species examined, when the first 2 gastral segments were abdominal segments 4 and 5, the sclerites of these segments were, without exception unfused (*Aenictus* workers, Ecitonini workers, the subfamilies Myrmicinae, Myrmeciinae, and Pseudomyrmecinae). When the 2 gastral segments were abdominal segments 3 and 4, segment 3 was fused, except in the males of *Neivamyrmex* and the workers of the subfamilies Dolichoderinae and Formicinae. In addition, in the Ponerinae, segment 4 was fused also.

Within the Ponerinae, the first and second gastral segments form an unexpandable gastral girdle. In the genera *Gnamptogenys* and *Rhytidoponera* the relationship of the tergite and sternite of abdominal segment 3 seemed to be intermediate between fusion and non-fusion. The sclerites pulled apart neatly along a "sutural" line but little membrane could be seen at the attachment of these 2 sclerites. Abdominal segment 4 of *Cerapachys* sp. and *Sphinctomyrmex steinheili* was likewise intermediately fused. Functionally these segments may be viewed as fused in that they provide little means for gaster expansion and are of a similar protective nature. In the Formicinae and Dolichoderinae, the unfused third abdominal segment contributes to the high degree of gastral expandibility present in these ants.

Phylogenetic Considerations

Wheeler indicated in 1928 that the family Tiphidae, in his estimation, was the most likely candidate among the solitary wasp families to have been ancestral to, or to have shared a common ancestry with, the Formicidae. Since that time, most hymenopterists have agreed with this conclusion, although in 1938, Morley still maintained that the Formicidae arose, through a "missing link," from mutillid stock. Wheeler and subsequent authors have discounted the Mutillidae as playing any role in the ancestry of the ants. Brown and Nutting (1950) have offered the following evidences of the close relationship between the tephritids and the ants: the presence of the first radial crossvein in the forewing of many tephritids (although weakly developed) and ants; the presence of primitive antennal segment numbers (13 in the male and 12 in the female); the development of the first antennal segment into a lengthened scape; the tendency toward the separation of the first postpropodeal segment from the remainder of the gaster by a constriction; and the tendency toward loss or weakening of the wings in the females. These authors found that the wings of *Anthobosca* (Tephritidae, Anthoboscinae) and *Plumarius* (Plumariidae) are quite antlike, but dismissed the latter as being ancestrally related to the ants because the male *Plumarius* (at that time only males had been described for the genus) lacks a number of other "protoformicid" features. Evans (1966), in describing the first *Plumarius* female, has concurred with this

decision and has indicated that *Anthobosca* still remains the better ant prototype. Brown and Nutting (1950) suggested that an early split in an evolutionary line may have occurred from which the formicids and anthoboscines arose, and that these anthoboscines were ancestral to the present day tiphiids. In 1933 Wheeler recorded that in personal communication, J. C. Bradley had favored the "Anthoboscidae" as being close to the ancestral Formicidae. Reid (1941), in his detailed analysis of the wingless hymenopteran thorax, concluded that a single tiphiid-like wasp was ancestral to the Formicidae "and at least half of Ashmead's Vespoidea." But in classifying the hymenopteran thorax into 3 major types, Reid (1941) also found that the ants were represented in all of these types. The recently discovered Mesozoic ant, *Sphecomyrma freyi*, has been characterized as being truly intermediate between primitive ants and the aculeate wasps (Wilson, Carpenter, and Brown, 1967). In comparing this ant with a number of modern aculeate families, it is closest to the Tiphidae, and in particular to *Methocha*. It is noteworthy that Wheeler (1928) dismissed the possibility that the "Methocidae" (along with the Mutillidae) were ancestrally close to the ants because the females were apterous. *S. freyi* differs significantly in 2 respects from the previously hypothesized formicid archetype. It has short, curved, bidentate mandibles instead of mandibles of medium length with serially arranged multiple teeth, and its petiole is strongly constricted behind instead of being broadly joined to the gaster.

The labra of the tiphiids examined share few characters with those of the ants. Tiphiid labra do not resemble those of ants, and all possess a series of very thick, long setae near or along their distal margins. Although the labra of *Rhagigaster unicolor* (fig. 23) and *Tachynomyia* sp. (fig. 27) are particularly unlike those of ants, the labrum of *Methocha stygia* (fig. 14) is not radically different from ant labra. In fact, it compares fairly well with the labrum of the queen of *Melissotarsus beccarii*, particularly with respect to the setae, although this resemblance is probably superficial. The *M. beccarii* labrum is deeply cleft, but that of *M. stygia* is only slightly emarginate.

If the primitive mandible of the ants is assumed to be like that of the tiphiids, particularly *Methocha* (fig. 16), and of *Sphecomyrma freyi*, it is most often seen in a similar condition in the sexual forms of the subfamily Dorylinae. Wilson *et al.* (1967) indicated that the mandibles of male amblyoponines are also like those of wasps. Consequently the primitive mandible appears to be preserved in some sexual ant forms, while the mandibles of workers must be considered derivative from this type. The worker mandibles of *Dorylus (Dichthadia) laevigatus* (fig. 156) and *D. (Typhlopone) dentifrons* (fig. 187) are somewhat wasplike in appearance, although it is difficult to determine whether these mandibles were derived from more broadly triangular ones or from wasplike types.

In the structure of the labrum, maxillae, and labium of the tiphiids examined, *M. stygia* most closely resembles the ants. This is particularly true

for the cardo (fig. 19), which in *Rhagigaster* (fig. 21) and *Tachynomyia* (fig. 28) is clearly unlike that in ants.

Until the recent discovery of *Sphecomyrma*, the fossil record of the ants has extended back only to the Eocene Epoch, or about 40 to 50 million years. Wheeler (1914) reported on ants of the Baltic amber (Oligocene Epoch) and concluded that differentiation of the ant worker caste must have been completed "not later than the Cretaceous or even the Jurassic or Triassic periods." Many of the genera described from the Tertiary fossil record are still represented today among the living ants. Wilson and Taylor (1964) have described a fossil ant colony of the genus *Oecophylla* discovered in lower Miocene deposits in Kenya. This colony contained worker subcastes whose polymorphism conforms to that of living *Oecophylla*, and this fact is submitted by Wilson and Taylor as evidence of the stability of "a specific social system" through a period of 30 million years or longer. The discovery of *Sphecomyrma* in amber of the Magothy formation has pushed back the fossil record of ants, and of the aculeate hymenoptera as well, to the Upper Cretaceous — or approximately 100 million years.

Two basic interpretations of phylogeny within the Formicidae exist in the literature: one, described by Wheeler (1928), in which the Ponerinae represent a primitive stock from which the other subfamilies radiated, and the other, formulated by Brown (1954), in which the ants divided early in their evolution into 2 complexes, the Poneroid and the Myrmecoid. Wheeler's hypothesis has been most recently supported by Robertson (1968) in a study of the venom apparatus in Hymenoptera, and Brown has been supported by Eisner (1957) in an investigation of the ant proventriculus.

The Ponerinae are generally regarded as a primitive group, and this idea is central to Wheeler's (1928) hypothesis regarding the origin of other ant subfamilies. Reid (1941) has pointed out that in thoracic characters the Ponerinae display by far the greatest diversity, which probably supports the view that they are the oldest group. Brown (1954) also indicated that the Ponerinae are an extremely heterogeneous group. This fact is borne out in an examination of the mouthparts. Palpal segmentation, the shape of the labrum, stipes, mandible, and galea all vary widely. Contrary to this trend, however, is the presence in some species of each tribe examined (except the Platythyreini) of the paraglossae and/or paraglossal sensory pegs. Also present in all tribes of Ponerinae is what appears to be a galeal comb. Again, however, it is not found in all species in each of the tribes.

Reid (1941) indicated that the thorax of some species of *Ectatomma* (Ponerinae) is similar to the typical myrmicine thorax. Subsequently other workers (Brown 1954; Brown and Kempf, 1967) have indicated that the myrmicines may have arisen from the Ectatommini near *Gnamptogenys*. Brown (personal communication) has indicated that if the second gastral segment were not fused in the ectatommines, weight would be lent to this argument, but the sclerites of this segment are fused in the ectatommines as they are in the other Ponerinae. Perhaps of greater significance is the

presence of paraglossae or paraglossal pegs in both the ponerines (including the ectatommines) and the myrmicines. Paraglossal lobes are found in only 1 species of those examined outside of these 2 subfamilies. It is striking that these structures should be totally lacking in the Cerapachyinae and Dorylinae, both considered phylogenetically close to the Ponerinae. The sensory pegs are identical in both subfamilies, and the paraglossae are quite similar, as can be seen in *Odontomachus rixosus* (fig. 333) and *Vollenhovia* n. sp. (fig. 341).

Though Brown (1954) maintained the Cerapachyinae as a distinct subfamily separated from the Ponerinae in his arrangement of the subfamilies into complexes, he and Nutting (1950) earlier indicated that this group is probably not deserving of subfamily rank. Reid has indicated that the Cerapachyinae are of one type of thorax and that they are close to the ponerine tribe Proceratiini. Kusnezov (1952) presented evidence that the cerapachyines were not ponerines, but his observations were based almost exclusively upon the genus *Acanthostichus*, doubtfully a cerapachyine. In mouthpart morphology, the cerapachyines superficially appear as a cohesive group. All possess a well developed transverse stipital groove, and all (except *Sphinctomyrmex*) have a similarly shaped 2-segmented maxillary palpus. But although the labra of *Cerapachys* (figs. 104, 107); and *Sphinctomyrmex* (fig. 118) are similar, those of *Acanthostichus* (fig. 102) and *Cylindromyrmex* (fig. 115) are quite different. Also, the transverse groove is not an exclusive character of the cerapachyines, but in only 1 ponerine species, *Amblyopone* sp., is it as well developed. In only one character, the unfused state of the sclerites of gastral segment 2, do the Cerapachyinae differ as a group from all the remaining Ponerinae (an intermediate condition with respect to fusion exists in *Cerapachys* sp. and *Sphinctomyrmex steinheili*). While their morphological similarities might be convergent responses to comparable raiding and foraging habits, forming an unrelated group of species, I would hesitate to place them back in the Ponerinae until more is known about their morphology and ethology.

Much attention has been given to the probable relationships between the Ponerinae, Dorylinae, and Cerapachyinae. Wheeler (1928) suggested that the Cerapachyinae served as an evolutionary link between the ponerines and dorylines, and Ashmead (1905) had earlier placed the genus *Acanthostichus* with the Dorylinae. Reid (1941) indicated that the development of the thorax did not support the view that the Cerapachyinae served as such a link, particularly since the thorax of *Dorylus* is less specialized than that of the Cerapachyinae. Brown and Nutting (1950), in examining wing venation, supported Reid's view. The proventriculus of the ponerines and cerapachyines is similar in construction, while that of the Dorylinae is reduced to the point where it consists of only the stomodaeal valve (Eisner, 1957).

Among the mouthpart characteristics, the galeal comb and the transverse stipital groove are most commonly shared by the Ponerinae, Cera-

pachyinae, and Dorylinae. The galeal comb is most strongly developed in the Ecitonini and *Acanthostichus* and appears in various degrees among numerous ponerines. The transverse groove is strongly developed in the Dorylini, Ecitonini, Cerapachyinae, *Amblyopone* sp., and weakly developed in some of the Ectatommini. It is difficult to attach phylogenetic importance to these characters, since they can be easily explained as the result of convergence. The sclerites of gastral segments 1 and 2 are fused in both segments only in the ponerines. Hermann (1967) has shown that the ponerines and dorylines differ in the construction of the sting apparatus, primarily in that the Dorylinae lack a sclerite called the furcula. This sclerite is curiously also lacking in *Simopelta oculata*, an ant that has evolved toward an army ant lifeform (Borgmeier, 1950; Gotwald and Brown, 1966).

Group predation, similar to that so highly developed in the Dorylinae, is not uncommon among both the Ponerinae and Cerapachyinae. Wilson (1958a) has distinguished true doryline behavior as being a combination of nomadism (emigration between temporary bivouacs) and group predation. Reports on group predation in the ponerines and cerapachyines are numerous. Wheeler (1936) reported on the termite raiders, *Megaponera* and *Termitopone*, and Hermann (1968) has described the raids of the latter genus. Levieux (1966) has analyzed in detail the raiding columns of *Megaponera foetens*. Clark (1941) and Wilson (1958b) have discussed the group raids of cerapachyines and Wilson (1958a) has found that species of *Leptogenys* (Ponerinae) combine both nomadism and group predation. These facts have led Wilson (1958a) to conclude that legionary behavior may have arisen several times independently among the ants, and that if so, legionary behavior must confer considerable selective advantage upon ants behaving in this way. One might thus also expect convergence among morphological characters associated with this type of behavior.

Brown (1954) has suggested that the family Dorylinae might possibly be diphyletic, and Reid (1941) has pointed out that there are 2 distinct types of worker thorax in this subfamily. One is typical of the Dorylini and another of the Ecitonini. *Leptanilla* is of the Dorylini type and *Aenictus* and *Cheliomyrmex* are of the ecitonine type. Except for *Leptanilla* and *Aenictus*, the doryline thorax is characterized by a large endophragmal pit anterior to the propodeal spiracle. Brown and Nutting (1950) reported that, with respect to wing venation, the Dorylinae may represent a line arising from a preponerine stock. Schneirla has contributed much to the understanding of the functional behavior patterns in the Dorylinae and has compared the patterns in the New and Old World army ants (1957).

The present study has shown that the tribes Dorylini, Aenictini, and Ecitonini are distinct and easily separable from one another solely on the basis of the mouthparts. Cheliomyrmecini and Ecitonini are extremely close, and together form a distinct, closely related group. Labral tubercles, the galeal comb, the transverse stipital groove, and the lateral shoulder of the stipes are all well developed. The lacinia and galea are of a consistent

shape, as is the labrum and stipes. The mouthparts of *Dorylus* throughout the several subgenera also indicate that this genus is a homogeneous, closely related group. The exceptional development of the galeal crown and the consistency in shape of the palpi, stipes, galea, and lacinia all convey this impression. *Aenictogiton* has been placed with the Dorylini in this investigation on the basis of its rounded labrum, its well developed galeal crown, the shape of its 1-segmented labial palpus, the shape of the stipes, and the presence of the transverse stipital groove. The drawings of the male *Aenictogiton* mouthparts (plate 37) should be compared with those of the males of *Dorylus* (*Typhlopone*) *fulvus* (plates 43, 44) and *Aenictus* sp. (plate 36). *Aenictus* also forms a uniform group, although the structure of the labrum and mandibles varies somewhat. The ecitonines and Dorylini share well developed labral tubercles and transverse stipital grooves. They are strikingly different, however, in the construction of the labrum, in the development of the galeal crown, and in the absence of the galeal comb in the Dorylini and its presence in the Ecitonini. The Aenictini exhibit a rounded lacinia, a reduced lacinial comb, and a less complex stipes. Labral tubercles are not present. Do the similarities within the tribes and the distinct differences between the tribes indicate that these groups diverged from a common ancestor early in their history, or rather that the Dorylinae are truly polyphyletic? This question is difficult to answer, although it would not be surprising to find that this group is triphyletic, particularly since army-ant lifeways have strong selective advantages.

Borgmeier (1953, 1955) has revised the New World army ants and has given generic status to the previous subgenera. Although *Dorylus* similarly contains several subgenera, it is not possible yet to determine whether these deserve equivalent generic rank. Wilson (1964) has revised the "true army ants" (mainly *Aenictus*) of the Indo-Australian area, so that *Dorylus* remains the only major doryline group to be taxonomically revised.

An examination of the mouthparts of the Leptanillinae has yielded little information regarding the placement of this small group. As Brown (1954) has indicated, discovery of these species is so highly fortuitous and their anatomical reduction so drastic that their true phylogenetic affinities may never be discovered.

The mouthparts of the Myrmicinae appear, at first glance, diverse. The variation in palpal segmentation, in development of the distal labral margin, and in the shape of the stipes convey this impression. The mouthparts of *Metapone truki* (plate 80) and *Melissotarsus beccarii* contribute greatly to this appearance of heterogeneity. In spite of this diversity, the presence of the paraglossae unifies the group. This subfamily can almost be defined on the basis of these structures, and, as noted before, they provide evidence of an evolutionary link between the Ponerinae and myrmicines. These structures are lacking only in *M. truki* and *M. beccarii*. Each paraglossa is provided with a single sensory peg, which may or may not be partly surrounded by protective setae.

Reid (1941) found the myrmicine thorax to be of basically one type, the major exception being the tribe Melissotarsini. With the exception of the Cephalotini, the myrmicine proventriculus is degenerate and similar to that of the Dorylinae (Eisner, 1957). Reid (1941) indicated that the Myrmicinae and Pseudomyrmecinae may be related, but Brown (1954) placed these subfamilies in different complexes. Brown (1954) also indicated that the myrmicines have retained some primitive characters of the ectatommines.

The Myrmeciinae were first given subfamily status by Clark (1954). These ants have been considered anatomically and ethologically conservative (Brown, 1954) and include perhaps the single most primitive known living ant, *Nothomyrmecia macrops*. *N. macrops* was described by Clark (1934) from 2 specimens and has never again been collected (Brown and Wilson, 1959a). Reid (1941) has described the thorax of *Myrmecia* as relatively unspecialized but not appearing any more primitive than that of *Dolichoderus*. The proventriculus of *Myrmecia* is similar to that in most other Hymenoptera; in these the damming of the crop is an active energy-consuming process (Eisner, 1957). Robertson (1968) has described the structure of the venom apparatus as being clearly ancestral to that of the Myrmicinae.

The mouthparts of *Myrmecia auriventris* (plates 86, 87), with the exception of the mandibles, are somewhat similar to those of the myrmicines, as well as the dolichoderines and formicines. The palpi are primitively segmented, and in that way resemble the dolichoderines and formicines. Other than these comparisons, little can be said about the affinities of these mouthparts. The labium has the most massive subglossal brushes among the ants.

The behavior of those pseudomyrmecines that are mutualistically associated with acacia trees has been exhaustively studied by Janzen (1966, 1967a, 1967b), but their taxonomic placement and phylogenetic affinities are still poorly understood. Brown (1954) placed the pseudomyrmecines in the Myrmecioid complex, feeling that their "ancestors were bimodally pedicellate Myrmeciinae of the same stock which gave rise to *Myrmecia* and *Prionomyrmex*." The thorax of the Pseudomyrmecinae is relatively unspecialized (Reid, 1941), and the proventriculus is similar to that of *Myrmecia* (Eisner, 1957).

The mouthparts of *Pseudomyrmex* (plate 88) give little indication of their affinities. Palpal segmentation is primitive, and thus similar in that respect to other myrmecioid subfamilies.

The Dolichoderinae and Formicinae are old, outwardly similar, but not necessarily related, subfamilies and are currently distinguished from one another by the presence of a circular acidopore in the formicines and the absence of such a structure in the dolichoderines (Hung and Brown, 1966). These external differences are correlated with much greater differences in

the internal glandular structures of the gaster and also in the proventriculus. Wheeler (1928) reported that the dolichoderines probably arose from the ponerines through the annectant genus *Aneuretus*. Indeed, Brown (1954) and Wilson, Eisner, Wheeler, and Wheeler (1956) have likewise recognized the ancestral relationship of *Aneuretus* to the dolichoderines, but have emphasized that *Aneuretus* is most likely annectant with *Nothomyrmecia*-like stock. Brown (1954) has indicated that the Aneuretini may also have given rise to the Formicinae, but he no longer favors this view (Wilson, *et al.*, 1967). Robertson (1968) has reported that the structure of the venom apparatus provides a direct link between the Ponerinae and Formicinae. Reid (1941) found the dolichoderine thorax of a generalized type like that of *Myrmecia* and reported no significant differences between the thoraces of the dolichoderines and formicines. An examination of wing venation does not contradict the conclusion that the formicines may have been derived from the dolichoderines (Brown and Nutting, 1950).

Palpal segmentation is mostly primitive throughout the Dolichoderinae and Formicinae, and there are no developments in mouthpart morphology that will separate them from one another or from the Myrmeciinae. The general configuration of the labrum, stipes, and galea and lacinia are often quite similar [e.g., *Dolichoderus attelaboides* (plate 89) and *Gigantiops destructor* (plate 92)]. The mouthparts of *Acropyga* sp. (plate 90) depart from the basic formicine type in construction of the mandible, labrum, and maxilla, in the presence of paraglossae, and in the reduction of the palpi. These developments may be expressions of the highly specialized, hypogaecic lifeways of the genus. *Acropyga* obligately attends root coccids on cacao, coffee, and bananas (Weber, 1944). [Forel (1893) placed the New World species of *Acropyga* in the subgenus *Rhizomyrma*, using among his subgeneric descriptive characters the presence of a 2-segmented maxillary palpus and a 3-segmented labial palpus. It is noteworthy that the Brazilian species dissected in this investigation has a 1-segmented maxillary palpus.] The presence of paraglossae in *Acropyga* (without sensory pegs) (fig. 356) is difficult to explain. It is not known whether they are homologous with the paraglossae of the ponerines and myrmicines or whether they are secondary developments peculiar to this genus.

The dolichoderines and formicines have exploited such adaptations as crop storage and regurgitative feeding, and they apparently possess generalized mouthparts. These generalized mouthpart characteristics, including primitive palpal segmentation, are probably correlated with epigaecic foraging behavior and utilization of liquid food sources such as plant exudates and homopteran honeydew. Eisner (1957) has shown that their proventriculus is particularly adapted for crop storage in that damming of the crop is accomplished passively with no expenditure of energy. Unlike other ants whose first and second gastral segments are the third and fourth abdominals, the sclerites of their first gastral segment are unused. This certainly facilitates gastral expansion for crop storage.

Conclusions

The problem of describing morphological characters as primitive or derivative, specialized or generalized, can be exceedingly difficult. Even if we carefully relate the terms primitive and derivative to organismal phylogeny and specialized and generalized to ecological adaptation, we cannot always be sure of placing a given morphological character correctly. An organism is the sum of its characters, some of which may be primitive, some derived, some specialized, and some generalized — all at the same time. The Ponerinae are indeed a primitive group of ants on the basis of numerous conditions; but, when examining the palpi we find that the number of segments is often reduced from the primitive number of 6 (maxillary) and 4 (labial). This condition is thus believed to be derivative; but it can also be considered specialized if the reduction is a response to ecological conditions. The dolichoderines and formicines, on the other hand, while displaying complex social patterns, have maintained a primitive palpal segmentation and possess other mouthpart structures (stipes, galea, lacinia) that are simple in design. These latter structures appear generalized, but are they primitive or derivative? Have they evolved from more complex structures or have they remained basically unchanged in their evolution?

It is easy to find confident statements in the literature proclaiming phylogenies based on comparative studies of single structures or small groups of structures. But we must wait for the accumulation of these studies before we can venture upon phylogenetic schemes with any degree of confidence. Perhaps one of the most underestimated biological phenomena today is convergence, despite frequent examples claimed in the literature. I have tried to point out the possibility of morphological convergence in ants adapted to an army-ant lifeway. Selective pressures for increased efficiency in army-ant-like behavior must be similar for all stocks, and the ants can respond in only so many ways to maximize their efficiency. Is it too surprising, then, that *Simopelta oculata* is one of 2 ponerines thus far studied that has lost the furcula from its sting apparatus (a ubiquitous character among the Dorylinae) and at the same time is like the army ant in its behavior? On the basis of the furcula's absence we might regard *Simopelta oculata* and the dorylines as closely related. Upon examining other characters we can be relatively sure that they are not.

With these arguments in mind, I shall discuss the mouthparts of ants in these terms. The ants most specialized in mouthpart development are the Ponerinae, Cerapachyinae, Dorylinae, and possibly the Leptanillinae. Somewhere intermediate between specialized and generalized are the Myrmicinae and Pseudomyrmecinae, and those most generalized are the Myrmeciinae, Dolichoderinae, and Formicinae. To describe what might be primitive and derivative it is necessary to speculate on what the morphology of the mouthparts of the hypothetical ant archetype might have been like. Drawing heavily from what is known of *Sphecomyrma freyi* and

Methocha stygia the following characters probably should be regarded as primitive:

1. Mandibles slender, short and falcate; possibly bidentate.
2. Labrum simple, distal margin rounded, not cleft or deeply emarginate.
3. Maxillary palpus of 6 segments.
4. Stipes broad and without distinctive sculpture; lateral shoulder poorly developed.
5. Cardo elongated, articulatory surface of distal end broadened and translucent.
6. Galea without a well developed crown and without many setae; maxillary comb present.
7. Lacinia without a well developed comb.
8. Labial palpus of 4 segments. -

Based on these criteria, the Myrmeciinae, Dolichoderinae, and Formicinae would be most primitive, Pseudomyrmecinae would be intermediate (closer to the primitive), and the Myrmicinae, Ponerinae, Cerapachyinae, and Dorylinae most derivative. The Leptanillinae combine characters in such a way as to make classification difficult. It should be remembered that these observations are based primarily on worker mouthparts, and that a comparative investigation of males and females might yield considerably more information.

Because of the possibility of convergent morphological development, evaluating similarity between groups is hazardous, but certain trends should be noted. Based on the presence of paraglossae, the Ponerinae and Myrmicinae appear related; but the ponerines, cerapachyines, and dorylines also share enough characters to appear as a related group. It is certainly possible that the ponerines, cerapachyines, and dorylines arose from a protoponeroid stock and that the myrmicines arose from the ponerines some time later. The Dolichoderinae and Formicinae are obviously similar (possibly convergently so), but the Leptanillinae, Myrmeciinae and Pseudomyrmecinae are difficult to relate to other groups. The Myrmeciinae do resemble, to some extent, the dolichoderines and formicines. As has previously been pointed out, the dorylines are tripartite, with differences among the 3 included groups greater than those separating the dolichoderines and formicines. Whether this indicates that these 3 doryline groups have been separated from a common stock very early in their history or that they arose separately from different lines is not known. It is suggested, however, that polyphyly should be seriously considered.

An examination of the gastral sclerites has yielded little information. The cerapachyines can be separated readily from the ponerines on this basis (second gastral segment unfused in the cerapachyines). The dolichoderines and formicines are seen to have maintained unfused first and second gastral segments to maximize crop storage efficiency. The Ponerines, in contrast (remembering that in all 3 of these subfamilies the first and

second gastral segments are the third and fourth abdominals) have the sclerites of both segments fused or tightly connected, a condition probably of considerable mechanical protective advantage among primarily predaceous ants.

The findings of this investigation do not substantially support either Wheeler's (1928) or Brown's (1954) views on the phylogeny of the ants (although subfamily grouping, based on mouthpart similarities, does tend to follow that of Brown, 1954). While mouthpart morphology does not strongly indicate the deep cleft proposed by Brown (1954) in the evolution of ants, it also does not show any particular links between the poneines and formicines as proposed by Wheeler (1928).

It seems reasonable to propose that even further study of ant and tiphiid mouthpart morphology and function might yield information of greater importance in understanding ant phylogeny. Ant mouthparts may also provide excellent diagnostic characters in revisions at the generic level or higher. The mouthparts have been little used in this respect, no doubt because it takes a great deal of time and effort to deal with these structures satisfactorily. It is hoped that this investigation will encourage the more extensive use of these characters by ant taxonomists.

Literature Cited

Ashmead, W. H.

1905. A skeleton of a new arrangement of the families, tribes and genera of the ants, or the superfamily Formicoidea. *Can. Entomol.* 37:381-384.

Barth, R.

1960. Ueber den Bewegungsmechanismus der Mandibeln von *Odonotomachus chelifer* Latr. (Hymenopt., Formicidae). *Acad. Bras. Cienc. Ann.* 32:379-384.

Borgmeier, T.

1950. A fêmea dichthadiiforme e os estádios evolutivos de *Simopelta pergandei* (Forel) e a descrição de *S. bicolor* n. sp. *Rev. Entomol.* 21:369-380.
1953. Vorarbeiten zu einer Revision der neotropischen Wanderameisen. *Stud. Entomol.* 2:51 pp.
1955. Die Wanderameisen der Neotropischen Region (Hym. Formicidae). *Stud. Entomol.* 3. 717 pp.
1957. Die Maxillar- und Labialtaster der Neotropischen Dorylinen (Hym., Formicidae). *Rev. Bras. Biol.* 17:387-394.

Brown, W. L., Jr.

1954. Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Insectes Soc.* 1:21-31.

- Brown, W. L., Jr., and Kempf, W. W.
1967. *Tatuidris*, a remarkable new genus of Formicidae (Hymenoptera). *Psyche* 74:183-190.
- Brown, W. L., Jr., and Nutting, W. L.
1949. Wing venation and the phylogeny of the Formicidae (Hymenoptera). *Amer. Entomol. Soc. Trans.* 75:113-132.
- Brown, W. L., Jr., and Wilson, E. O.
1959a. The search for *Nothomyrmecia*. *West. Aust. Natur.* 7(2):25-30.
- Brown, W. L. Jr., and Wilson, E. O.
1959b. The evolution of the dacetine ants. *Quart. Rev. Biol.* 34:278-294.
- Bugnion, E.
1924. Le sac infrabuccal et le pharynx des fourmis. *Soc. Biol. Compt. Rend.* 91:998-1000.
1925. Notes relatives a la terminologie des organes buccaux des insectes. *Soc. Zool. France Bul.* 50:352-358.
1930. Les pièces buccales, le sac infrabuccal et le pharynx des fourmis. *Soc. Roy. Entomol. Egypte. Bul.* 14:85-210.
- Chatin, J.
1887. Recherches morphologiques sur les pièces mandibulaires, maxillaires et labiales des hyménoptères. Gauthier-Villars, Imprimeur-libraire, Paris. 41 pp.
- Clark, J.
1934. Notes on Australian ants, with a description of new species and a new genus. *Nat. Mus. Victoria. Mem.* 8:5-46.
1941. Australian Formicidae. Notes and new species. *Nat. Mus. Victoria. Mem.* 12:71-94.
1951. The Formicidae of Australia. I. Subfamily Myrmeciinae. *C. S. I. R. O., Melbourne, Austr.* 230 pp.
- Cohic, F.
1948. Observations morphologiques et écologiques sur *Dorylus (Anomma) nigricans* Illiger. *Rev. Franç. Entomol.* 14:229-276.
- Crampton, G. C.
1923. A phylogenetic comparison of the maxillae throughout the orders of insects. *New York Entomol. Soc. J.* 31:77-107.
1928. The eulabium, mentum, submentum and gular region of insects. *J. Entomol. Zool.* 20:1-18.
- DuPorte, M.
1967. Morphology of the first and second maxillae of insects. *Can. J. Zool.* 45:1269-1273.
- Eisner, T.
1957. A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). *Mus. Comp. Zool. Harvard. Bul.* 116:439-490.

Eisner, T., and Happ, G. M.

1962. The infrabuccal pocket of a formicine ant: a social filtration device. *Psyche* 69:107-116.

Ettershank, G.

1966. A generic revision of the world Myrmicinae related to *Solenopsis* and *Pheidologeton* (Hymenoptera: Formicidae). *Aust. J. Zool.* 14:73-171.

Evans, H. E.

1966. Discovery of the female *Plumarius* (Hymenoptera, Plumariidae). *Psyche* 75:229-237.

Forel, A.

1874. Les fourmis de la Suisse. *Soc. Helvetique Sci. Natur. Mem.* 26:452 pp.
1893. Formicides de l'Antille St. Vincent. *Trans. Entomol. Soc. London.* Part 4: 333-418.
1928. The social world of the ants compared with that of man. Vol. I. Translated by C. K. Ogden. G. P. Putnam's Sons, Ltd., London. 551 pp.

Gotwald, W. H., Jr., and Brown, W. L., Jr.

1966. The ant genus *Simopelta* (Hymenoptera: Formicidae). *Psyche* 73:261-277.

Hermann, H. R., Jr.

1968. Group raiding in *Termitopone commutata* (Roger) (Hymenoptera: Formicidae). *Georgia Entomol. Soc. J.* 3:23-24.

Hermann, H. R., Jr., and Blum, M. S.

1967. The morphology and histology of the hymenopterous poison apparatus. III. *Eciton hamatum* (Formicidae). *Entomol. Soc. Amer. Ann.* 60:1282-1291.

Hollingsworth, M. J.

1960. Studies on the polymorphic workers of the army ant *Dorylus* (*Anomma*) *nigricans* Illiger. *Insectes Soc.* 7:17-37.

Hung, A. C. F., and Brown, W. L., Jr.

1966. Structure of gastric apex as a subfamily character of the Formicinae (Hymenoptera: Formicidae). *New York Entomol. Soc. J.* 74:198-200.

Huxley, T. H.

1878. A manual of the anatomy of invertebrated animals. D. Appleton and Company, New York. 596 pp.

Janet, C.

1899. Essai sur la constitution morphologique de la tête de l'insect. Georges Carré et C. Naud, Éditeurs, Paris. 74 pp.
1904. Observations sur les fourmis. Limoges, Imprimerie-librairie Ducourtieux et Gout., Paris. 68 pp.
1905. Anatomie de la tête du *Lasius niger*. Limoges, Imprimerie-librairie Ducourtieux et Gout., Paris. 40 pp.

Janet, C. (*continued*)

1911. Constitution morphologique de la bouche de l'insecte. Limoges, Imprimerie-librairie Ducourtieux et Gout., Paris. 35 pp.

Janzen, D. H.

1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20:249-275.
1967a. Fire, vegetation structure, and the ant \times Acacia interaction in Central America. *Ecology* 48:26-35.
1967b. Interaction of the bull's-horn Acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in Eastern Mexico. *Univ. Kansas Sci. Bul.* 47:315-558.

Kellog, V. L.

1902. The development and homologies of the mouthparts of insects. *Amer. Nat.* 36:683-706.

Kusnezov, N.

1951. Los segmentos palpaes en hormigas. *Folia Univ., Cochabamba, Bolivia* 5:62-70.
1952. La posición sistemática de la subfamilia Cerapachyinae (Hymenoptera, Formicidae). *Dusenía* 3:115-117.
1954a. Phyletische Bedeutung der Maxillar- und Labialtaster der Ameisen. *Zool. Anzeiger* 153:28-38.
1954b. La formula palpal en las hormigas (Nuevos datos y algunas interpretaciones) (Hymenoptera: Formicidae). *Dusenía* 5:255-258.

Kutter, H.

1948. Beitrag zur Kenntnis der Leptanillinae. Eine neue Ameisengattung aus Sued-Indien. *Mitt. Schweiz. Entomol. Ges.* 21:286-295.

Levieux, J.

1966. Note préliminaire sur les colonnes de chasse de *Megaponera foetens* F. (Hyménoptère Formicidae). *Insectes Soc.* 13:117-126.

Liu, C. L.

1925. Observations on the acroglossal buttons and on the submentum of Hymenoptera. *Entomol. Soc. Amer. Ann.* 18:445-455.

Lubbock, J.

1877. On some points in the anatomy of ants. *Monthly Microscop. J.* 18:121-142.

Marcus, H.

1944. Estudios mirmecologicos. I. Estudio comparado de la articulacion mandibular en las hormigas y termites. *Acta Zool. Lilloana* 2:259-284.
1945. Estudios mirmecologicos. IV. Las articulaciones "trampas" en las mandibulas de los Odontomachini. *Rev. Agr.* 2(3):13-20.

Matsuda, R.

1965. Morphology and evolution of the insect head. Amer. Entomol. Inst., Ann Arbor, Mich. 334 pp.

Morley, B. D. W.

1938. An outline of the phylogeny of the Formicidae. Bul. Soc. Entomol. France. 43:190-194.

Mukerji, D.

1933. On the anatomy of the worker of the ant *Dorylus (Alaopone) orientalis* Westw. Zool. Anzeiger. 105:97-105.

Pavan, M., and Ronchetti, G.

1955. Studi sulla morfologia esterna e anatomia interna dell' operaia di *Iridomyrmex humilis* Mayr e ricerche chimiche e biologiche sulla iridomirmecina. Atti Soc. Ital. Sci. Natur. 94:379-477.

Reid, J. A.

1941. The thorax of the wingless and short-winged Hymenoptera. Roy. Entomol. Soc. London. Trans. 91:367-446.

Rettenmeyer, C. W.

1963. Behavioral studies of army ants. Univ. Kansas. Sci. Bul. 44: 281-465.

Robertson, P. L.

1968. A morphological and functional study of the venom apparatus in representatives of some major groups of Hymenoptera. Austral. J. Zool. 16:133-166.

Savigny, J.

1816. Mémoires sur les animaux sans vertèbres. Part I., Fasc. 1. Théorie des organes de la bouche des crustacés et des insectes. Gabriel Dufour, Paris. 239 pp.

Schneirla, T. C.

1949. Army-ant life and behavior under dry-season conditions. 3. The course of reproduction and colony behavior. Amer. Mus. Natur. Hist. Bul. 94:1-81.
1957. A comparison of species and genera in the ant subfamily Dorylinae with respect to functional pattern. Insectes Soc. 4:259-298.

Snodgrass, R. E.

1928. Morphology and evolution of the insect head and its appendages. Smithsonian Misc. Coll. 81(3):158 pp.
1935. Principles of insect morphology. McGraw-Hill Book Co., Inc., New York. 667 pp.

Spangler, H. G., and Rettenmeyer, C. W.

1966. The function of the ammochaetae or psammophores of harvester ants, *Pogonomyrmex* spp. Kansas Entomol. Soc. J. 39:739-745.

Weber, N. A.

1944. The neotropical coccid-tending ants of the genus *Acropyga* Roger. Entomol. Soc. Amer. Ann. 37:89-122.

Wheeler, G. C., and Wheeler, E. W.

1930. Two new ants from Java. *Psyche* 37:193-201.

Wheeler, W. M.

1910. *Ants. Their structure, development and behavior.* Columbia Univ. Press, New York. 663 pp.

1914. The ants of the Baltic amber. *Schrift. Phys.-ökon. Ges. Königsberg* 55:1-142.

1923. *Social life among the insects.* Harcourt, Brace and Company, New York. 375 pp.

1928. *The social insects.* Harcourt, Brace and Company, New York. 378 pp.

1933. *Colony-founding among ants.* Harvard Univ. Press, Cambridge. 179 pp.

1936. Ecological relations of ponerine and other ants to termites. *Amer. Acad. Arts Sci. Proc.* 71:159-243.

Wheeler, W. M., and Bailey, I. W.

1920. The feeding habits of pseudomyrmine and other ants. *Amer. Phil. Soc. (n.s.) Trans.* 22:235-279.

Wilson, E. O.

1955. A monographic revision of the ant genus *Lasius*. *Mus. Comp. Zool. Harvard Bul.* 113:1-199.

1958a. The beginnings of nomadic and group-predatory behavior in the ponerine ants. *Evolution* 12:24-36.

1958b. Observations on the behavior of the cerapachyine ants. *Insectes Soc.* 5:129-140.

1964. The true army ants of the Indo-Australian area. *Pacific Insects* 6:427-483.

Wilson, E. O., Carpenter, F. M., and Brown, W. L., Jr.

1967. The first Mesozoic ants, with the description of a new subfamily. *Psyche* 74:1-19.

Wilson, E. O., Eisner, T., Wheeler, G. C., and Wheeler, J.

1956. *Aneuretus simoni* Emery, a major link in ant evolution. *Mus. Comp. Zool. Harvard. Bul.* 115:85-99.

Wilson, E. O., and Taylor, R. W.

1964. A fossil ant colony: new evidence of social antiquity. *Psyche* 71:93-103.

Acknowledgments

I wish to express my deepest appreciation to the members of my Special Committee at Cornell University for the guidance provided throughout my graduate studies. This committee was composed of Dr. William L. Brown, Jr. (Chairman), Dr. William C. Dilger, and Dr. Thomas Eisner. I am especially indebted to Dr. Brown for his continued interest in my research and for his generous support, not only in terms of time, but also financially through National Science Foundation Grants GB-2175 and GB-5574X. Thanks are due Dr. George C. Eickwort and Mr. David Barr, Cornell University, for carefully reading the manuscript and providing me with detailed critiques of the writing. I am also grateful to Dr. John G. Franclemont, Cornell University, for his patient counsel throughout the period of this research.

To each of the following persons, I wish to express my thanks for their generous contributions of specimens: Dr. Roger D. Akre, Washington State University; Mr. Robert G. Beard and Mr. Rossiter H. Crozier, Cornell University; Dr. Henry R. Hermann, Jr., University of Georgia; Mr. Akey C. F. Hung and Dr. Paul B. Kanno, University of North Dakota; Dr. David H. Kistner, Chico State College, California; M. Jean Levieux, École Normale Supérieure, Paris; Dr. John C. Moser, U.S.D.A., Southern Forest Experiment Station, Pineville, Louisiana; Mr. Robert W. Poole, Cornell University; Dr. Carl W. Rettenmeyer, Kansas State University; Mr. George Rotramel, University of California at Berkeley (Mr. Rotramel supplied me with numerous species of tiphiids which, in turn, had been kindly given to him by Mr. B. B. Given, Nelson, New Zealand and by Mr. E. F. Riek, C.S.I.R.O., Canberra, Australia); Dr. T. C. Schneirla, American Museum of Natural History, New York; Mr. Robert E. Silberglied, Cornell University; and Dr. Neal A. Weber, Swarthmore College.

I collected many of the specimens examined in this investigation on a Cornell University field expedition to Mexico in the summer of 1965. The expedition was supported by National Science Foundation Grant GB-2175 (W. L. Brown, Jr., Principal Investigator). Other specimens came from the Cornell University Collection and the Museum of Comparative Zoology, Harvard University.

I am deeply grateful to my wife, Joanna, for typing the several drafts of the manuscript and for her kind and patient encouragement throughout the conduct of this research.